

African Plant Diversity Systematics and Sustainable Development



Proceedings of the XIXth AETFAT Congress

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(editors)

26 SEP. 2013

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African Plant Diversity
Systematics and Sustainable Development
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Diversité des Plantes Africaines
Systématique et Développement Durable
Actes du XIX^e Congrès AETFAT,
tenu à Antananarivo, Madagascar, 26–30 Avril 2010



B 133683

Meise
National Botanic Garden of Belgium

Scripta Botanica Belgica

Miscellaneous documentation

published by the National Botanic Garden of Belgium

Series editor: E. Robbrecht

Volume 50

Natacha Beau, Steven Dessein and Elmar Robbrecht (eds)

African Plant Diversity, Systematics and Sustainable Development

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CIP Royal Library Albert I, Brussels

African Plant Diversity, Systematics and Sustainable Development – Proceedings of the XIXth AETFAT Congress, held at Antananarivo, Madagascar, 26–30 April 2010. Natacha Beau, Steven Dessein and Elmar Robbrecht (eds) – Meise, National Botanic Garden of Belgium, 2013. – viii + 424 pp.; 28 × 21 cm. – (Scripta Botanica Belgica, Vol. 50)

ISBN 9789072619921

ISSN 0779-2387

D/2013/0325/003

Cover design: Sven Bellanger

Cover photographs: Petra De Block, Steven Dessein

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Printed in Belgium



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For contributions in French, the English translation of the title is given between brackets.
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Pour les contributions en français, une traduction en anglais du titre est donnée entre crochets.
L'astérisque () indique que l'article a été pré-publié dans Plant Ecology and Evolution.*
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Foreword

When Prof. Vololoniaina H. Jeannoda, and Dr. Sylvain G. Razafimandimbison, General Secretaries of AETFAT, welcomed the participants of the nineteenth AETFAT Congress, they expressed the hope that “this Congress will be an opportunity for each one of us to highlight to the world the value and importance of African plant diversity”. The launched theme of the Congress, African plant diversity, systematics and sustainable development, referred to this.

Initially AETFAT (“Association pour l’Étude Taxonomique de la Flore d’Afrique Tropicale”) was a contact forum for taxonomists and flora writers. Its focus gradually widened into the whole field of botany. The nineteenth meeting was the AETFAT Congress with the most complex programme ever. A total of twelve symposia were organized, some of them with subsessions. Almost 500 presentations (oral and poster) were made. Such a volume was problematic for the continuation of the AETFAT tradition to publish the results of the Congress in a single Proceedings book. As editors we therefore felt that rapid publications of the Proceedings would be a tremendous task, especially because we wanted to watch over quality by applying peer review to all submissions. In order to enhance rapid publication of the most valuable contributions, it was therefore decided to prepublish these in *Plant Ecology and Evolution*. In 2011–2013, a total of sixteen papers appeared in volumes 144–146 of the journal.

Eighty-seven submissions were received. After peer review, 34 manuscripts were accepted for the present Proceedings, apart from the sixteen ones prepublished. Inevitably, the reduction from almost 500 to fifty contributions made the structure of the symposia too intricate to be kept for the organization of the Proceedings.

The following reorganization was made for the present Proceedings. We arranged the papers in themes as consistently as possible – some presentations at a certain symposium were therefore moved to a different theme here. The sequence of the themes keeps systematics and phytogeography at the center of the interest of AETFAT but also illustrates the link of these disciplines with areas that nowadays have a prominent importance, global change and conservation.

1. **Global change** (corresponding to symposium 6 ‘African plants and global change’)
2. **Conservation** (partially corresponding to symposium 8.2 ‘Sustainable use and conservation of African plants’)
3. **Ecology and vegetation** (corresponding to symposium 3 ‘Ecology of African plants’)
4. **Systematics** (with contributions from the symposium 1.1 ‘Systematics of higher plants (Pteridophyta and Spermatophyta)’).
5. **Phytogeography** (with contributions from the symposium 2 ‘Phytogeography of African plants’)
6. **Floristics** (being a part wherein the purely floristic contributions from the symposia 1.1 ‘Systematics of higher plants (Pteridophyta and Spermatophyta)’ and 1.2 ‘Systematics of Algae, Fungi and Bryophytes’ are assembled)
7. **Databases** (corresponding to the symposium 7 ‘African plants databases’)
8. **Sustainable use** (for part of the contributions from symposium 8.2 ‘Sustainable use and conservation of African plants’)
9. **Ethnobotany** (corresponding to symposium 8.1 ‘Ethnobotany of African plants’).

Three submissions were received from the symposium 9 ‘Aloes of the world’. They were placed under the themes 4, 6 and 7, matching the content of each contribution. Three submissions came from the symposium 11 ‘Biogeography of Madagascar’ and were placed under themes 2, 5 and 7.

No submissions were received from the specialist symposia 4 ‘Reproductive biology of African plants’, 10 ‘Rubiaceae’ and 12 ‘Anatomy and dendrochronology of African plants’. No papers were neither submitted from the symposium 5 ‘Progress on African floras’; this topic is repeated at every AETFAT congress but consequently not reflected in the present Proceedings. The success of the theme Databases is illustrative for the present-day shift from printed floras to electronic tools.

While we prepared these Proceedings for the printing house, the news of the decease of Professor Jean Léonard reached us. Jean Léonard was the last survivor of the founders of AETFAT. We want to bring him a tribute here, recalling his importance for our Association. These Proceedings thus end with a short biographic note.

Many chairpersons at the symposia accepted to also act as guest editors for the present Proceedings. The editorial team of the XIXth AETFAT Proceedings book are grateful for their help.

The editors

Avant-propos

Lorsque les secrétaires généraux de l'AETFAT, Prof. Vololoniaina et Dr. Sylvain G. Razafimandimbison, accueillirent les participants au dix-neuvième Congrès de l'AETFAT, ils é mirent le voeu que "ce Congrès sera une opportunité pour chacun d'entre nous de mettre en exergue aux yeux du monde entier la valeur et l'importance de la diversité végétale africaine". Le lancement du thème du Congrès, Diversité des plantes africaines, systématique et utilisation durable, adresse cela.

A l'origine, AETFAT ("Association pour l'Étude Taxonomique de la Flore d'Afrique Tropicale") était un forum de rencontres pour les taxonomistes et les rédacteurs de flores. Son objectif s'élargit graduellement vers le champ large de la botanique. La dix-neuvième rencontre fut le Congrès AETFAT comportant le programme le plus complexe. Douze symposia au total furent organisés, certains d'entre eux comportant des sous-sessions. Environ 500 présentations orales ou posters furent réalisées. Un tel volume de contributions posait problème si nous voulions suivre la tradition consistant à publier les résultats du Congrès dans un livre unique. En tant qu'éditeurs, nous ressentîmes que la publication rapide du livre des Actes serait une tâche phénoménale, d'autant plus que nous souhaitions contrôler la qualité de toutes les contributions en appliquant une relecture par des pairs. Pour permettre une publication rapide des meilleures contributions, nous décidâmes de pré-publier ces contributions dans la revue *Plant Ecology and Evolution*. De 2011 à 2013, un total de seize articles parurent dans les volumes 144 à 146 de la revue.

Nous reçûmes 87 soumissions. Après relecture par les pairs, 34 manuscrits furent acceptés pour ce livre des Actes, sans compter les seize soumissions déjà pré-publiées. Inévitablement, la réduction drastique (de 500 à cinquante contributions) ne permit pas de conserver la structure originale des symposia pour organiser le contenu du livre.

Nous avons donc ré-organisé le contenu pour ce livre des Actes. Les contributions ont été classées par thèmes, de manière aussi cohérente que possible – certaines présentations, enregistrées dans un symposium précis ont donc été déplacées vers un autre thème dans le présent livre. La séquence des thèmes fait la part belle à la systématique et à la phytogéographie, qui sont les centres d'intérêts majeurs de l'AETFAT, mais illustre également le lien entre ces disciplines et d'autres domaines présentant une importance actuelle accrue: les changements globaux et la conservation.

1. **Changements globaux** (correspondant au symposium 6 'Plantes africaines et changements globaux')
2. **Conservation** (correspondant partiellement au symposium 8.2 'Utilisation durable des plantes africaines et conservation')
3. **Ecologie et végétation** (correspondant au symposium 3 'Ecologie des plantes africaines')
4. **Systématique** (avec des contributions provenant du symposium 1.1 'Systématique des plantes supérieures (Pteridophyta et Spermatophyta)').
5. **Phytogéographie** (avec des contributions provenant du symposium 2 'Phytogéographie des plantes africaines')
6. **Floristique** (comprenant quelques contributions purement floristiques provenant des symposia 1.1 'Systématique des plantes supérieures (Pteridophyta et Spermatophyta)' et 1.2 'Systématique des Algues, des Champignons et des Bryophytes')
7. **Bases de données** (correspondant au symposium 7 'Bases de données sur les plantes africaines')
8. **Utilisation durable** (une partie des contributions provenant du symposium 8.2 'Utilisation durable des plantes africaines et conservation')
9. **Ethnobotanique** (correspondant au symposium 8.1 'Ethnobotanique des plantes africaines').

Trois soumissions provenaient du symposium 9 'Aloes du monde'. Elles furent placées sous les thèmes 4, 6 et 7, pour correspondre au contenu de chaque contribution. Trois soumission provenant du symposium 11 'Biogéographie de Madagascar' furent placées sous les thèmes 2, 5 et 7.

Nous n'avons reçu aucune contribution provenant des symposia spécialisés 4 'Biologie de la reproduction des plantes africaines', 10 'Rubiaceae' et 12 'Anatomie et dendrochronologie des plantes africaines'. De même, nous n'avons reçu aucune contribution provenant du symposium 5 'Progrès sur les flores africaines'; ce sujet est récurrent dans chaque Congrès AETFAT, mais n'est donc pas représenté dans ce livre. Le succès du thème Bases de données reflète le glissement actuel des flores publiées sur papier vers les outils électroniques.

Pendant que nous préparions ces Actes pour l'imprimerie, nous avons appris le décès du professeur Jean Léonard. Il était le dernier cofondateur de l'AETFAT encore en vie. Nous voulons lui rendre hommage ici en rappelant son rôle pour notre Association. Vous trouverez une courte notice biographique à la fin de ces Actes.

De nombreux facilitateurs des symposia ont accepté notre invitation et sont devenus des rédacteurs associés pour la publication de ce livre. L'équipe de rédaction du livre des Actes du XIX^e congrès de l'AETFAT les remercie pour leur aide précieuse.

Les rédacteurs



The genus *Acacia* (Fabaceae) in East Africa: distribution, diversity and the protected area network

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Background and aims – Plants are often overlooked in conservation planning, yet they are the foundation of all terrestrial ecosystems. The East Africa region is used to investigate the effectiveness of protected areas for conserving plants. With a wide range of ecosystems and 771 protected areas covering nearly one quarter of the land area, East Africa is an ideal location to assess the effectiveness of protected areas through distribution modelling of the genus *Acacia*.

Methods – Herbarium specimen data (2,047 records) were collated from East Africa for 65 taxa (species, subspecies, varieties) from the genus *Acacia*. Generalised Additive Models were used to determine climatic drivers, and thence to extrapolate climatic suitability across the region. For two *Acacia* taxa, we investigated the potential for climate-induced range-shifts using a downscaled regional climate model under two IPCC scenarios.

Key results – Approximately two thirds of *Acacia* diversity hotspots had < 10% coverage by protected areas. Furthermore, the protected area network covered less of the predicted ranges of the *Acacia* taxa and contained fewer taxa per unit area than would be expected under randomised placement. Areas with suitable climate for high-elevation, moisture-dependent taxa such as *A. abyssinica* subsp. *calophylla* are predicted to contract their potential range by up to 80% towards mountain peaks, where protected areas are dominated by low-level protection forest reserves. Conversely, the area of suitable environment for a xerophytic low-elevation species (*A. turnbulliana*) is predicted to increase by up to 77%.

Conclusions – East Africa's national parks may not be preserving an important component of ecosystem diversity, a situation exacerbated by climate change. Even within the genus *Acacia*, different species are predicted to respond differently to climate change. Priority areas for research and conservation are identified based on overlap between predicted high *Acacia* diversity and gaps in the collection record, with northern and eastern Kenya highlighted as particularly important. High elevation protected areas are also predicted to become increasingly important as climatic refugia in a warmer future.

Key words – gap analysis, climate change, nature reserve, *Senegalia*, species distribution model, *Vachellia*.

INTRODUCTION

The majority of Africa's protected areas were established in response to declining large animal numbers since the early 20th century (Balmford et al. 1992). Only recently have more broadly defined biodiversity metrics been used to establish

areas for the protection of nature or natural resources (Lockwood et al. 2006, Marshall et al. 2007). Plants have long been overlooked in the design of protected area systems (Jaffré et al. 1998, Vargas et al. 2004, Burgess et al. 2005), despite their role as the foundation of all terrestrial ecosystems, harnessing the sun's energy and thus providing nutrition for

the entire food chain. Plants are the structural component of habitats, providing shelter and nesting sites for animals, as well as contributing to climate-change mitigation through carbon sequestration and moderation of nutrient and hydrological flows. As conservation continues to develop a 'biodiversity for livelihoods' mandate, information on plant distributions and the ways in which ecosystems will respond to future climatic and economic developments is crucial.

Distribution modelling is one of a range of tools used to predict suitable environmental conditions for a taxon (hereafter used to mean a species, subspecies, or variety) across a landscape based on limited information (fig. 1). Environmental conditions at locations of known taxon occurrence are used to parameterise a niche or multidimensional envelope that can be used to infer the suitability of other geographic locations across a broader region. The application of Distribution Models (hereafter, DMs) is increasingly far-reaching, and includes use for managing resources, predicting the spread of invasive species/pathogens, predicting the impacts of climate change, and planning the design of protected area networks (Franklin 2010). DMs are particularly useful where logistical difficulties such as poor infrastructure or large geographic scale preclude full inventories. DMs also allow for the exploration of 'what if' scenarios, in the present case exploring the impact of climate change on current species distribution.

A major aim in designing a reserve network is to conserve the maximum level of biodiversity based on available resources. However, reserve design cannot consider every species in an ecosystem, particularly in the tropics, where the numbers of species involved are extremely high. There are, for example, approximately 12,500 plant species in the area covered by the *Flora of Tropical East Africa* (Kenya, Tanza-

nia, and Uganda) alone (Beentje & Smith 2001, H. Beentje, Royal Botanic Gardens, Kew, UK, pers. comm.). An alternative to measuring absolute biodiversity is to determine a set of indicator taxa whose presence signals high overall biodiversity in an area. An ideal indicator taxon should: be easily recognisable and easy to locate, be found in reasonable densities, not be highly mobile, have a high degree of specialisation, and be representative of a fully functional ecosystem (Caro & O'Doherty 1999, Hilty & Merenlender 2000). Many species of plants fulfil these criteria but have traditionally been less often used than faunal indicators.

The genus name *Acacia* Mill. is here applied broadly, including the segregate genera *Senegalia* Raf. and *Vachellia* Wight & Arn., but excluding *Faidherbia* A.Chev. Under this circumscription, *Acacia* includes a number of species that dominate the structure and floristic composition of extensive areas of East African woodland, wooded grassland and bushland (Pratt & Gwynne 1977, Coe & Beentje 1991). The genus occurs across a wide range of ecosystems, from arid deserts to montane forests, with growth forms that include small shrubs, lianas and large trees (New 1984). There are 64 species of *Acacia* known from the five eastern African countries of Burundi, Kenya, Rwanda, Tanzania and Uganda (Dharani 2006). None of these species have been assessed as globally threatened (IUCN 2011); however very few of them have been evaluated by the IUCN Red List process and many occur in woodland habitats that are threatened by anthropogenic influence, particularly charcoal production, burning, livestock damage and agricultural encroachment (New 1984, Sinclair et al. 2008). These habitats are mostly unprotected by legislation and have therefore received little attention in previous regional biodiversity assessments. As one of the better studied plant genera in Africa, *Acacia* also

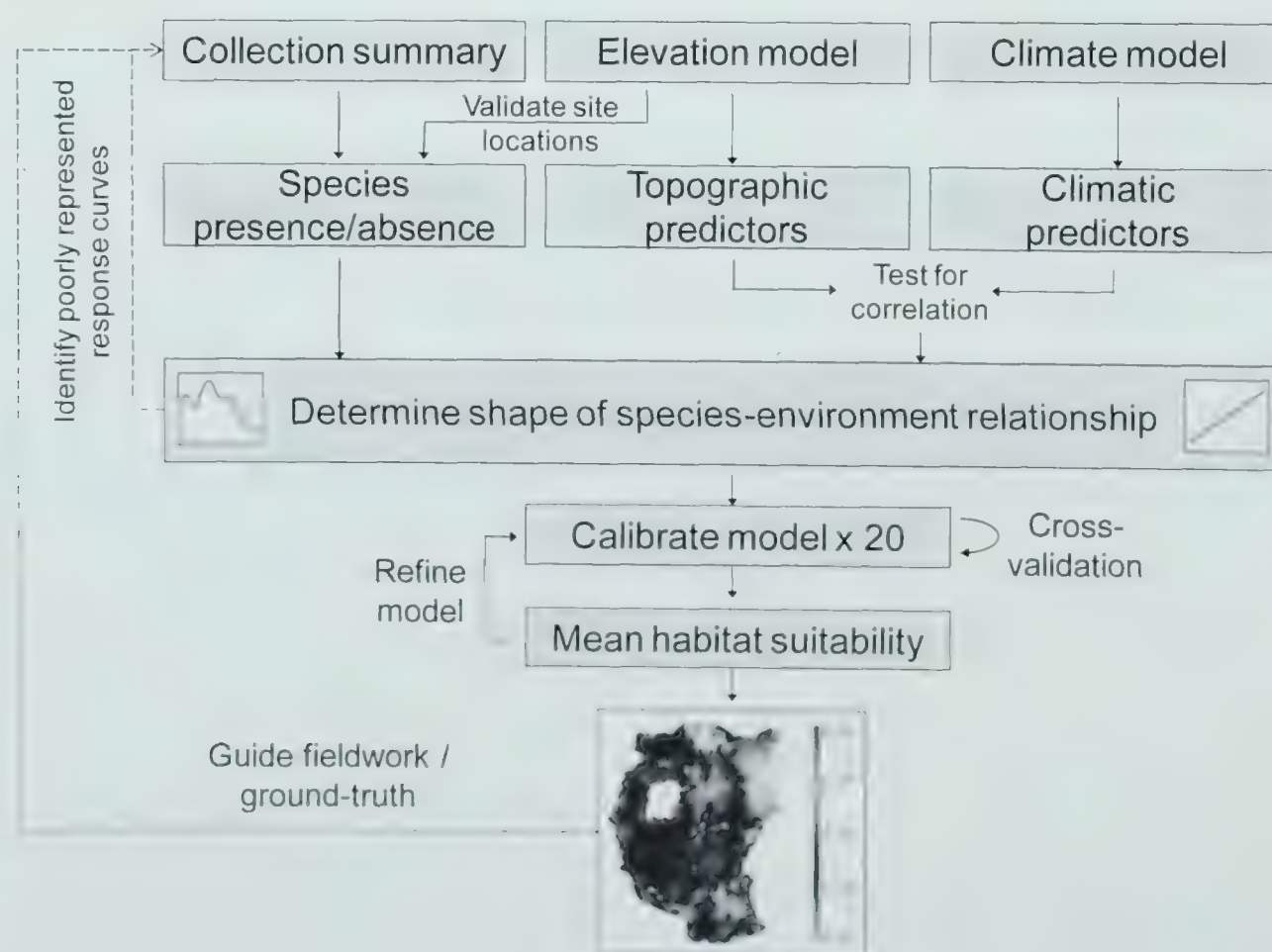


Figure 1 The process of distribution modelling (adapted from Platts et al. 2008).

has an advantage for data acquisition in that it has been well curated in a number of major herbaria (in particular, the East African Herbarium, the Royal Botanic Gardens, Kew, and the Missouri Botanical Garden), with reliable identification and associated meta-data.

The aim of this paper is to predict the present day distribution of *Acacia* in East Africa and to establish how well members of the genus are conserved under the current protected area network. The various taxa are modelled against climatic and topographic variables and their spatial distributions extrapolated to the broader landscape. A composite of the most successfully modelled taxa is then used to estimate the geographic distribution of *Acacia* diversity in relation to protected areas. Regional climate forecasts are used to estimate the potential impact of climate change on future *Acacia* distribution and how this changed distribution will interact with protection areas. Finally, we make suggestions for geographical priorities for management and taxonomic research.

MATERIAL AND METHODS

Study area

The region used for modelling included the five eastern East African countries of Burundi, Kenya, Rwanda, Tanzania and Uganda (defined here as ‘East Africa’). East Africa was selected for its wide range of ecosystems, extensive areas of unsurveyed or logistically difficult landscape, and also for its globally recognised importance for wildlife tourism. The area contains 771 protected areas, covering 23.3% of the total land area, including 65 world-renowned national parks and game reserves (UNEP-WCMC 2009), which attract approximately 3.5 million tourists annually (<http://www.statistics.eac.int>). Despite the outstanding importance of biodiversity, tourism and cultural resources in the East African region, biological data that are essential for setting conservation priorities are not currently available in a format that managers can use, being spatially incomplete and deposited in widely scattered museum collections. Rapidly growing human populations and increasing land fragmentation have restricted wildlife and pastoral movements across much of East Africa, causing range loss and aggravating effects of periodic drought (Western & Manzanillo Nightingale 2004). Compounding these human impacts, the extent and speed of climate change in the area pose a serious threat to the natural capital that is vital to individual livelihoods and national economies.

Data collation and refinement

A total of 2,047 *Acacia* herbarium records were collated from 65 taxa and 46 species (59 taxa excluding species also represented at infraspecific level; table 1). Our data include 71.9% of the 64 *Acacia* species known from the region (Dharani 2006). Collection data were collated from five herbaria: East African Herbarium, National Museums of Kenya (Nairobi); Royal Botanic Gardens, Kew (UK); Missouri Botanical Garden (USA); National Herbarium of Tanzania (Arusha); University of Dar es Salaam (Tanzania). We collated environmental data for the region at a spatial resolution of 1 arc-minute. Environmental variables included mean and

range in annual temperature, mean annual rainfall, potential evapotranspiration (PET), maximum water deficit, slope, and aspect. Details are given as supplementary material (electronic appendix 1).

Model calibration and performance

Distribution data consisted only of presence records for each taxon. We also generated pseudo-absence data to constrain the models (Phillips et al. 2009; electronic appendix 1). The probability of occurrence of each taxon in 1 arc-minute grid cells was determined based on Generalised Linear or Additive Models (GLM/GAM) of taxon presence versus environmental conditions. Since collection data were too sparse to partition into independent sets for training and testing, we used cross-validation to assess generality. We also assess envelope uncertainty as the proportional difference between extreme values of each climate variable and the known range at collection localities (Envelope Distance Maps, EDMs). See the supplementary material for full explanation of model calibration and performance (electronic appendix 1).

Biodiversity and protection

Estimates of *Acacia* taxon richness (hereafter termed ‘*Acacia* diversity’) were based on the spatial predictions of all robust models ($n=45$). Predictions were considered robust if and only if (1) both sensitivity and AUC_{cv} exceeded 0.7, (2) the modelled response shapes were biologically plausible (i.e. with no more than one point of inflection), and (3) the spatial predictions were in agreement with known distributions according to collection locations and the most recent *Acacia* field guide (Dharani 2006).

Presence-absence maps were derived from the probability surfaces by maximising the sum of sensitivity and specificity (Liu et al. 2005). These binary predictions were then summed across taxa and averaged across the ten model runs to give an estimate of *Acacia* diversity. We focussed on two subsets of taxa with robust predictions: (1) those with excellent agreement between collection locations and predicted climate suitability, and (2) these same ‘excellent’ taxa plus those with range extensions compared with collection records and/or the most recent field guide (Dharani 2006), which we define as ‘good’. Probability surfaces were considered ‘poor’ where collection records were lacking from the most extensive geographic locations of predicted climate suitability. Models defined as poor were not used in biodiversity estimates. Geographic locations corresponding to the upper quartiles of richness estimates were used to indicate hotspots of *Acacia* diversity.

Acacia diversity predictions were compared to the spatial distribution of three levels of protected area. In decreasing order of strength, the protected area levels assessed were (1) IUCN protected area management category I-IV (excluding forest reserves, which are not typically guarded by patrols and in many instances have high levels of habitat degradation due to illegal activity; e.g. Ahrends et al. 2010), (2) IUCN category V-VI (including forest reserves I-IV), and (3) protected areas not internationally recognised (UNEP-WCMC 2009). To determine a quantitative estimate of the

Table 1 – Distribution modelling summary for 65 *Acacia* taxa.

Columns show the number of 1 min grid cells in which a taxon was recorded (n), cross-validated AUC score (AUC_{cv}), percentage deviance explained (%D), proportion of presences (sens) and pseudo-absences (spec) predicted correctly by the models, and the level of constraint to areas of known distribution according to collection locations (conf1) and the most recent field guide (conf2; Dharani 2006).

*Eighteen taxa with excellent fit to collections. † 24 taxa with good fit to collections plus minor range extensions (parentheses indicate taxa removed from biodiversity calculation due to species/infraspecies overlap either within () or between [] the good and excellent model subsets).

Indicator taxon	n	AUC _{cv}	%D	sens	spec	conf1	conf2
<i>Acacia abyssinica</i> subsp. <i>calophylla</i> *	26	0.94	0.61	0.97	0.86	Excellent	Good
<i>Acacia adenocalyx</i> †	32	0.92	0.66	0.95	0.90	Good	Good
<i>Acacia amythethophylla</i>	29	0.71	0.26	0.63	0.76	NA	NA
<i>Acacia ancistroclada</i> †	12	0.91	0.79	0.99	0.94	Good	Good
<i>Acacia ataxacantha</i> †	17	0.83	0.55	0.88	0.87	Good	Good
<i>Acacia brevispica</i> subsp. <i>brevispica</i>	83	0.65	0.35	0.74	0.58	NA	NA
<i>Acacia burtii</i> †	11	0.91	0.78	0.99	0.94	Good	Good
<i>Acacia bussei</i> †	36	0.85	0.59	0.93	0.82	Good	Excellent
<i>Acacia dolichocephala</i>	8	NA	NA	NA	NA	NA	NA
<i>Acacia drepanolobium</i> †	60	0.74	0.34	0.73	0.74	Good	Poor
<i>Acacia elatior</i> †	26	0.88	0.62	0.90	0.84	Good	Good
<i>Acacia elatior</i> subsp. <i>elatior</i>	7	NA	NA	NA	NA	NA	NA
<i>Acacia elatior</i> subsp. <i>turkanae</i>	19	0.89	0.61	0.94	0.87	Poor	No data
<i>Acacia etbaica</i> subsp. <i>platycarpa</i>	21	0.67	0.49	0.77	0.78	NA	NA
<i>Acacia fischeri</i> †	11	0.87	0.66	0.97	0.89	Good	Good
<i>Acacia gerrardii</i> *	139	0.76	0.41	0.81	0.67	Excellent	Good
<i>Acacia gerrardii</i> var. <i>calvescens</i>	16	0.74	0.45	0.91	0.73	Poor	NA
<i>Acacia gerrardii</i> var. <i>gerrardii</i> (*)	86	0.74	0.29	0.70	0.78	Excellent	NA
<i>Acacia gerrardii</i> var. <i>latisiliqua</i> [†]	26	0.93	0.74	0.98	0.90	Good	NA
<i>Acacia goetzei</i> (†)	48	0.79	0.47	0.84	0.72	Good	Poor
<i>Acacia goetzei</i> subsp. <i>goetzei</i> †	30	0.75	0.48	0.83	0.73	Good	NA
<i>Acacia goetzei</i> subsp. <i>microphylla</i> †	24	0.85	0.59	0.91	0.86	Good	NA
<i>Acacia hamulosa</i>	6	NA	NA	NA	NA	NA	NA
<i>Acacia hockii</i>	136	0.67	0.43	0.79	0.56	NA	NA
<i>Acacia horrida</i> subsp. <i>benadirensis</i> *	25	0.91	0.70	0.97	0.90	Excellent	Good
<i>Acacia kirkii</i> subsp. <i>kirkii</i> *	31	0.81	0.41	0.88	0.76	Excellent	Good
<i>Acacia laeta</i> *	19	0.79	0.44	0.78	0.87	Excellent	Good
<i>Acacia lahai</i> †	28	0.96	0.72	0.98	0.90	Good	Good
<i>Acacia mbuluensis</i>	4	NA	NA	NA	NA	NA	NA
<i>Acacia mellifera</i> (*)	155	0.71	0.19	0.77	0.62	Excellent	Good
<i>Acacia mellifera</i> subsp. <i>detinens</i>	11	0.81	0.61	0.86	0.90	Poor	Poor
<i>Acacia mellifera</i> subsp. <i>mellifera</i> *	140	0.73	0.30	0.73	0.69	Excellent	Good
<i>Acacia montigena</i> *	25	0.91	0.55	0.94	0.87	Excellent	Good
<i>Acacia nigrescens</i>	15	0.81	0.45	0.85	0.78	Poor	Poor
<i>Acacia nilotica</i> subsp. <i>leiocarpa</i> *	17	0.89	0.67	0.97	0.93	Excellent	NA
<i>Acacia nilotica</i> subsp. <i>subalata</i>	178	0.62	0.35	0.66	0.61	NA	NA
<i>Acacia oerfota</i> †	24	0.72	0.44	0.80	0.81	Good	Good
<i>Acacia paolii</i> *	41	0.88	0.65	0.88	0.86	Excellent	Excellent
<i>Acacia paolii</i> subsp. <i>paolii</i>	5	NA	NA	NA	NA	NA	NA
<i>Acacia paolii</i> subsp. <i>paucijuga</i>	4	NA	NA	NA	NA	NA	NA
<i>Acacia persiciflora</i> *	30	0.94	0.72	0.98	0.90	Excellent	Excellent
<i>Acacia pilispina</i>	8	NA	NA	NA	NA	NA	NA
<i>Acacia polyacantha</i> subsp. <i>campylacantha</i>	114	0.69	0.33	0.68	0.65	NA	NA
<i>Acacia pseudofistula</i> *	29	0.88	0.68	0.99	0.89	Excellent	Good
<i>Acacia reficiens</i> subsp. <i>misera</i> *	10	0.89	0.69	0.95	0.92	Excellent	Excellent
<i>Acacia robusta</i> subsp. <i>usambarensis</i> †	46	0.75	0.27	0.78	0.75	Good	Poor
<i>Acacia royumae</i>	13	0.89	0.71	0.98	0.90	Excellent	Good

Table 1 (continued) – Distribution modelling summary for 65 *Acacia* taxa.

Indicator taxon	n	AUC _{cv}	%D	sens	spec	conf1	conf2
<i>Acacia schweinfurthii</i> var. <i>schweinfurthii</i> †	13	0.78	0.63	0.88	0.92	Good	Poor
<i>Acacia senegal</i> var. <i>leiorhachis</i> †	11	0.75	0.60	0.96	0.83	Good	NA
<i>Acacia senegal</i> var. <i>senegal</i>	88	0.66	0.36	0.70	0.64	NA	NA
<i>Acacia seyal</i>	51	0.60	0.36	0.67	0.64	NA	NA
<i>Acacia seyal</i> var. <i>fistula</i>	21	0.63	0.44	0.70	0.77	NA	NA
<i>Acacia seyal</i> var. <i>seyal</i>	24	0.62	0.41	0.65	0.72	NA	NA
<i>Acacia sieberiana</i> var. <i>sieberiana</i> †	20	0.80	0.59	0.90	0.87	Good	NA
<i>Acacia sieberiana</i> var. <i>woodii</i> *	46	0.80	0.51	0.78	0.82	Excellent	NA
<i>Acacia stuhlmannii</i>	33	0.68	0.50	0.79	0.70	NA	NA
<i>Acacia tanganyikensis</i> †	16	0.90	0.63	0.99	0.88	Good	Good
<i>Acacia thomasii</i> †	24	0.82	0.54	0.96	0.75	Good	Good
<i>Acacia tortilis</i> subsp. <i>raddiana</i>	4	NA	NA	NA	NA	NA	NA
<i>Acacia tortilis</i> subsp. <i>spirocarpa</i>	56	0.68	0.41	0.82	0.59	NA	NA
<i>Acacia turnbulliana</i> *	10	0.99	0.92	1.00	0.99	Excellent	Excellent
<i>Acacia xanthophloea</i> *	17	0.80	0.55	0.88	0.85	Good	Good
<i>Acacia zanzibarica</i> (†)	49	0.85	0.54	0.81	0.86	Good	Good
<i>Acacia zanzibarica</i> var. <i>microphylla</i> †	15	0.93	0.77	0.98	0.96	Good	NA
<i>Acacia zanzibarica</i> var. <i>zanzibarica</i> †	29	0.84	0.58	0.86	0.85	Good	NA

protected area coverage in *Acacia* diversity hotspots, we calculated the degree of overlap (area and proportion) between the 36 predicted ranges and the protected area network. *Acacia* taxa were deemed likely to be present in an area if presence was predicted in five or more model runs. The areas and proportions were averaged over all taxa and 95% confidence limits calculated (999 bootstraps). We then used a binomial test (Crawley 2005) to determine whether the mean proportion of *Acacia* taxon range protected was significantly different to the proportion of the region covered by protected areas (23.3%, UNEP-WCMC 2009). This binomial test allowed us to estimate whether the protection of *Acacia* taxa range was significantly different to a randomised placement of protected areas.

Climate change

Model predictions were extrapolated into the future for the montane tree *Acacia abyssinica* Hochst. ex Benth. subsp. *calophylla* Brenan and for the xerophytic lowland tree *A. turnbulliana* Brenan. These two taxa were chosen for their contrasting ecology and their reliable prediction compared with known distributions.

Climate scenarios for 2020, 2055 and 2090 were derived from the Global Circulation Model ECHAM5, and were subsequently downscaled via the Regional Climate Model REMO (Potsdam Institute for Climate Impacts Research, Germany). We used two scenarios from the Fourth Assessment Report of the International Panel for Climate Change (IPCC-AR4, IPCC 2007). The first of these (scenario A1B) represents an increase in global temperature, peaking mid-century, following a minor reduction in greenhouse gas emissions. The second (scenario B1) is a less pessimistic scenario with global population equivalent to scenario A1B, but with more rapid improvement in public services and economic structures. Under scenario A1B, the East African regional

temperature is predicted to increase by mean 3.8 ± 0.2 s.d. °C (min 3.0, max 5.0) by 2090, and under scenario B1, by mean 2.6 ± 0.1 s.d. °C (min 1.8, max 3.9). These represent the two most divergent scenarios up to 2060 in terms of temperature and atmospheric CO₂ (IPCC 2007) and hence provide upper and lower estimates of predicted climate change.

Future climate data were downscaled from 0.5 to 0.0167 decimal degrees (30 arc-minutes to 1 arc-minute; 1.85 km) by imposing the forecast change-factors (REMO anomalies) upon the baseline temperature and rainfall grids (WorldClim and TRMM, respectively) used to model present-day distributions (Platts 2012).

Nomenclature of the *Acacia* taxa

The circumscription and nomenclature of the *Acacia* taxa (species, subspecies, varieties) in this paper (see Table 1) follows that of Brenan (1959), revised in accordance with the following treatments:

Brenan (1970): *A. brevispica* Harms subsp. *brevispica*, *A. montigena* Brenan & Exell, *A. robusta* Burch. subsp. *usambarensis* (Taub.) Brenan, *A. senegal* (L.) Willd. var. *leiorhachis* Brenan.

Asfaw & Thulin (1989): *A. amythethophylla* Steud. ex A. Rich., *A. hamulosa* Benth., *A. oerfota* (Forssk.) Schweinf., *A. paolii* Chiov. subsp. *paolii*, *A. paolii* Chiov. subsp. *paucijuga* Brenan, *A. sieberiana* DC. var. *woodii* (Burt Davy) Keay & Brenan.

RESULTS

Acacia distribution: (a) taxa

Models of predicted current distribution were produced for 58 *Acacia* taxa (51 excluding species/infraspecies overlap; table 1, electronic appendix 2), each with records of occur-

rence spanning ten or more unique grid cells in the East African region. Of these, 45 taxa (40 excluding overlap) were robust according to validation statistics (AUC_{cv} 0.70-0.99; sensitivity 0.70-0.99). The predictive success of these models is further supported by expert knowledge on the distribution of *Acacia*: 18 taxa (16 excluding overlap) produced models very similar to known distributions, and a further 23 (21 excluding overlap) produced models largely in agreement with known distributions but with some range extension (table 1, fig. 2, electronic appendix 2). Four taxa showed poor comparison to known distributions and were dropped from further analyses [*Acacia elatior* Brenan subsp. *turkanae* Brenan, *A. gerrardii* Benth. var. *calvescens* Brenan, *A. mellifera* (Vahl) Benth subsp. *detinens* (Burch.) Brenan and *A. nigrescens* Oliv.].

Envelope distance was found to be high only at the summits of Mt. Kilimanjaro and Mt. Kenya, where models were forced to extrapolate down to 52.3% below the parameter range of the training data (electronic appendix 3). Maximum water deficit and annual precipitation also showed uncertainty up to 65.0% above the parameter range in the hottest and driest parts of northeast Kenya (electronic appendix 3). These knowledge gaps highlight both environmental and spatial bias in the herbarium record (fig. 3A, table 2). In particular, northern and eastern Kenya, southern and west-central Tanzania and western Uganda have the fewest *Acacia* records.

Acacia distribution: (b) biodiversity and protection

Acacia diversity estimates are presented for the 16 taxa that showed excellent fit to known distributions, and then combined with 20 of the taxa that showed minor range extension to known distributions (table 1, fig. 3; the 20 taxa reduced from 21 to account for species/infraspecies overlap with the first 16 taxa).

Among the herbarium records, 40 of the 51 *Acacia* taxa (78.4%) have been recorded from protected areas in IUCN categories I-IV, excluding forest reserves (46 in IUCN I-VI; 48 in all protected areas). However, of considerable management importance is that many of the predicted *Acacia*-rich areas (fig. 3C & D) were outside of the current protected area network (fig. 3B). Of the 17 potential hotspots identified for the genus (fig. 3C & D, table 2), 11 (64.7%) have low coverage by protected areas (0–10% geographic area) and seven (41.1%) have no overlap with IUCN category I-VI protected areas. Per unit area, the number of taxa predicted to occur in protected areas (IUCN I-VI: 3.96 ± 0.01 ; non-IUCN protected areas: 4.03 ± 0.01 km⁻²; all protected areas: 3.99 ± 0.01 km⁻²) is less than for East Africa as a whole (4.05 ± 0.002 km⁻²).

The predicted ranges of the 36 *Acacia* taxa used in biodiversity mapping lay predominantly outside the protected area network (21.6%; table 3, electronic appendix 4), leaving an average of 78.4% (237.0 km²) of ranges unprotected. Comparing this proportion of protection to the protected area coverage of the East Africa region (23.3%) reveals that the

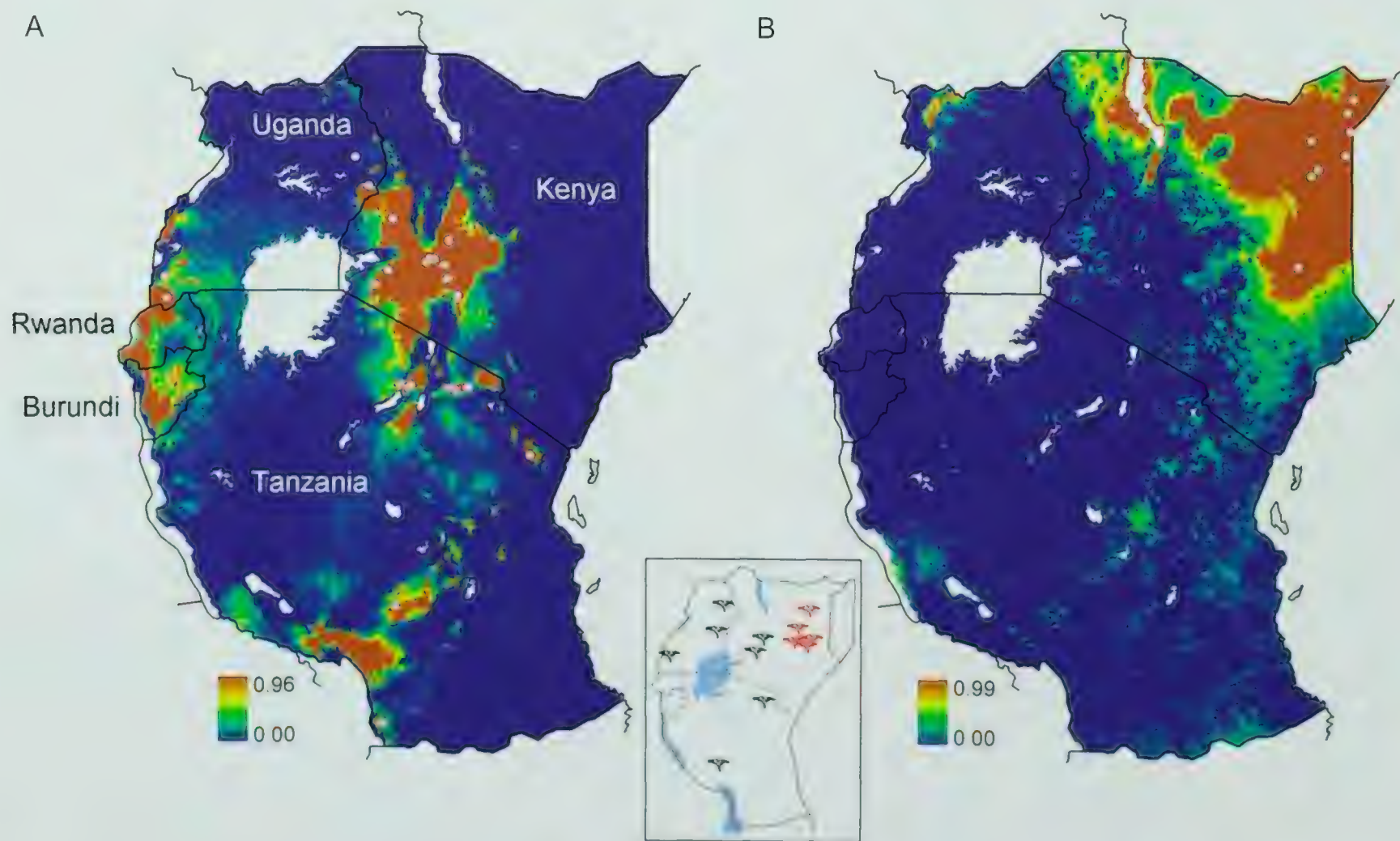


Figure 2 Predicted habitat suitability for: A, *Acacia abyssinica* subsp. *calophylla* and B, *Acacia turnbulliana*. Scale bars indicate mean suitability from ten repeated model runs. Pink dots indicate presence localities used to develop the models. Inset shows known distribution of *A. abyssinica* subsp. *calophylla* (black tree icons) and *A. turnbulliana* (red), adapted with permission from Dharani (2006).

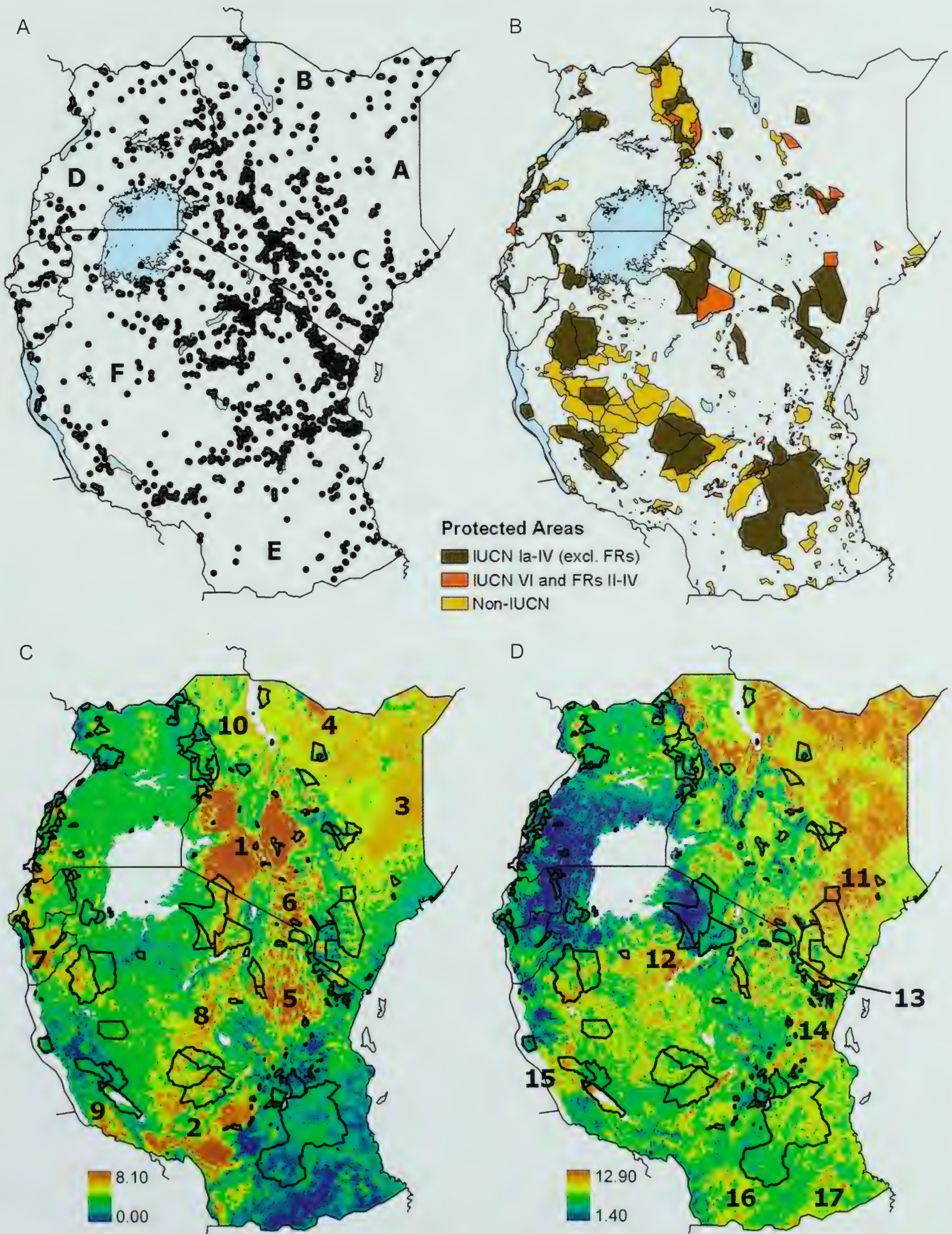


Figure 3 – Location of: A, *Acacia* collection records and B, protected areas in East Africa. Predicted biodiversity of the genus *Acacia* is shown in relation to IUCN protected areas I-VI for: C, sixteen taxa with excellent fit to known distributions and D, 36 taxa including the same sixteen taxa plus twenty taxa showing minor range extensions to known distributions. Letters A–F (in A) indicate geographic areas under-represented in the herbarium record and numbers 1–17 (in C & D) indicate *Acacia* biodiversity hotspots (table 2). Scale bars indicate the predicted number of *Acacia* taxa per 1 arc-minute (1.85 km) grid cell averaged across ten model runs.

Table 2 - Summary of the 17 geographic areas identified as high priorities for research and conservation of the genus *Acacia* in East Africa (see fig. 3C & D).

Letters A–F refer to areas under-represented in the herbarium record (see fig. 3A).

*Protected areas coverage defined as low (< 10%), moderate (10–30%) or high (> 30%).

**Saadani National Park established in 2005 has protected status equivalent to IUCN class I/II, but had not been assessed for the World Database of Protected Areas (UNEP-WCMC 2009).

Code Fig. 3	Location	Protected Area Coverage*	Collection Record	Biodiversity Importance	
				Best 16 taxa	Best 36 taxa
1	Southwest Kenya	Low	Good	High	Moderate
2	Central-south Tanzania	Moderate	Moderate	High	Moderate
3 / A	East Kenya	None	Poor	High	High
4 / B	Marsabit, Kenya	Low	Poor	High	High
5	West Manyara / Maasai Steppe, Tanzania	Low	Moderate	High	Moderate
6	South-central Kenya	Low	Good	High	High
7	South-west Uganda to Kigoma, Tanzania	Moderate	Moderate	High	Low
8	Singida, Tanzania	Low	Moderate	High	Moderate
9	South Rukwa to south-west Mbeya, Tanzania	Very Low	Moderate	High	Low
10	Turkana, Kenya	Nil	Moderate	Mod-High	High
11 / C	Tana River, Kenya	Moderate	Poor-Mod	Moderate	High
12	Central Shinyanga / north-east Tabora, Tanzania	Low	Moderate	Low-Mod	High
13	Mkomazi	High	Low	Moderate	High
14	North Pwani / south Tanga, Tanzania	Low**	Good	Moderate	High
15	West Rukwa, Tanzania	Moderate	Moderate	Low	High
16	Central Ruvuma, Tanzania	Very Low	Poor	Moderate	Mod-High
17	West Mtwara / south-west Lindi, Tanzania	Low	Moderate	Low	Mod-High
D	East Uganda	Moderate	Poor	Moderate	Low
E	South Tanzania (includes Central Ruvuma, 16)	Moderate	Poor	Low	Moderate
F	East-central Tanzania	High	Poor	Moderate	Mod-High

level of protection is no more than would be expected by randomised placement (Binomial test: $\chi^2 = 0.74$, $p = 0.39$). A mean of 11.2% of the predicted range of each species was protected within the highest category of protected area (IUCN I-IV, excluding forest reserves). *Acacia* taxon ranges are marginally more often conserved in IUCN protected areas (12.6%) than non-IUCN protected areas (8.9%; table 3). Five *Acacia* taxa [*A. horrida* (L.) Willd. subsp. *benadirensis* (Chiov.) Hillc. & Brenan, *Acacia gerrardii* var. *latisiliqua* Brenan, *A. reficiens* Wawra subsp. *misera* (Vatke) Brenan, *A. turnbulliana* and *A. zanzibarica* S. Moore var. *microphylla* (Taub.) Brenan] have less than 10% of their predicted range included within a protected area, four of which occurred predominantly in north-east Kenya.

Climate change

Climate change projections suggest a decline in climatic suitability up to 80.0 % (163,574 km² declining to 32,630 km²; scenario A1B) or 65.2 % (56,848 km²; scenario B1) by 2090 for *Acacia abyssinica* subsp. *calophylla* (fig. 4A, electronic appendix 5A). This tree is typically found at high elevation, where the atmosphere is moist and temperatures are cool. Accordingly, the various DM runs for *A. abyssinica* subsp. *calophylla* identified negative relationships with tempera-

ture (annual mean and PET, %D 30.4, contributing to all ten forward-backward models runs), and positive relationships with the annual moisture index (%D 52.9, 6/10 runs). The future projection for *A. abyssinica* subsp. *calophylla* predicts a progressive movement to higher elevation, where the most common protected areas are forest reserves (2090: 18.3% of range protected under IUCN reserve versus 27.4% non-IUCN; fig. 4A). Because of the steep predicted range decline, the proportion of area protected is predicted to increase (21.4 % increasing to 52.4% [A1B] or 37.9% [B1] in 2090; fig. 4A).

The lowland tree *Acacia turnbulliana* is predicted to increase in range by 77.0% (122,395 km² increasing to 532,675 km²; scenario A1B) or 63.1% (331,414 km²; scenario B1) by 2090 (fig. 4B; appendix 5B [online material]). The increase resulted from a positive relationship with temperature (annual mean and PET, %D 59.4, 7/10 runs; temperature range, %D 28.2, 6/10 runs) and a negative relationship with the moisture index (%D 67.2, 3/10 runs). However, these (monotonic) relationships (fig. 4B) were extrapolated up to 12.7% (A1B, 2090) beyond present-day temperatures in East Africa, and thus the projected range-expansion in north-east Kenya is subject to envelope distance up to 18.3% for mean temperature (electronic appendix 3). From being the least

Table 3 – Mean ($\pm$ 95% bootstrapped confidence limit) of the predicted range of 36 *Acacia* taxa within protected areas in East Africa (total area 1,711,585 km²).

*There are no IUCN class V protected areas in the region.

	Area of predicted range protected (thousand km ²)	% of predicted range protected
IUCN I-IV (excluding Forest Reserves)	35.6 (28.4–42.8)	11.2 (9.8–12.7)
IUCN VI and IUCN Forest Reserves*	4.1 (3.3–4.8)	1.4 (1.1–1.8)
IUCN total (I-VI)	39.7 (32.3–47.1)	12.6 (12.2–14.1)
Non-IUCN protected areas	28.5 (21.2–35.6)	8.9 (7.3–10.6)
All protected areas	68.2 (55.5–83.7)	21.6 (18.6–24.4)
Unprotected	237.0 (204.6–269.4)	78.4 (75.8–81.1)

protected *Acacia* taxon based on distribution models (0.4 % range within protected areas; electronic appendix 4), the projected range increase predicts an expansion into protected areas (16.7% [A1B] or 7.3% [B1] of predicted range in 2090; fig. 4A).

DISCUSSION

Acacia distribution and biodiversity

Many of the high *Acacia* diversity areas identified have not previously been highlighted as being of major importance for conservation of the genus. Botanists working in East Africa agree that these areas are likely to be important for *Acacia* species (N. Dharani, World Agroforestry Centre, Kenya, pers. comm.; R.E. Gereau pers. obs.), providing support for model outputs that were both robust and had good agreement with collection localities (fig. 3, table 2, electronic appendix 2).

Identification of biodiversity hotspots can help managers prioritise future conservation efforts (Myers et al. 2000). In determining conservation priorities for a taxon, the degree of protection of the overall range is more important than information on the location of isolated records. Thus, while many *Acacia* taxa have been collected from protected areas, there is discordance between protected areas and predicted *Acacia* diversity hotspots, low protection of predicted ranges (mean 78.4% unprotected; table 3) and extremely weak protection for taxa restricted to north-east Kenya. An increasing demand in East Africa for natural resources such as charcoal (Ahrends et al. 2010), fuelwood, honey, etc., leaves species outside of protected areas at risk. The designation of Africa's national parks and game reserves based on declining animal populations (Balmford et al. 1992) might therefore be failing to protect one of Africa's most iconic plant groups, which could in turn impact on East Africa's globally important vertebrate assemblage *via* the supporting function that *Acacia* species provide for habitat, herbivores and biogeochemical cycling.

Discordances between biologically rich areas and the protected area network in Africa have also been documented for threatened mammals (Fjelds  et al. 2004), birds (De Klerk et al. 2004) and threatened and/or range-restricted plants (Burgess et al. 2005). It is appropriate, therefore, to question the extent to which the genus *Acacia* is a suitable surrogate for overall biodiversity in the East African region. Pratt &

Gwynne (1977) delineated six eco-climatic zones in Kenya, Tanzania and Uganda based on moisture indices derived from monthly rainfall and evaporation. These eco-climatic zones are well correlated with vegetation and land-use classes, and each one is represented by a number of characteristic species, many of which belong to the genus of *Acacia* (Pratt & Gwynne 1977). We therefore assume that the distribution of these indicators represents a significant proportion of regional biodiversity. For example, bird assemblages in East Africa are dependent on the structure and diversity of woody plants for food and shelter (Kissling et al. 2010), while the interactions between *Acacia* trees, large herbivores, beetles, ants and other invertebrates are also well documented (New 1984). Predominantly associated with East African woodlands, wooded grasslands and bushlands, the genus *Acacia* is perhaps less representative of biodiversity in moist forest habitats, such as the Eastern Arc Mountains of Tanzania and Kenya. In addition, while hotspots 6 and 10 in fig. 3C conform to known biodiversity of woody vegetation in Kenya, more northern areas may not (Kissling et al. 2010). Nevertheless, this charismatic genus can be added to a growing body of evidence for hotspots of diversity situated outside of Africa's protected areas.

Many of the predicted *Acacia* climate suitability maps (electronic appendix 2) show reasonable fit to known distributions. However, as is typical for DMs, limiting factors beyond the scope of the models, combined with geographic gaps in the herbarium record, resulted in some degree of extension beyond known ranges (cf. Dharani 2006). Future botanical collection would be most beneficial in areas where *Acacia* diversity is predicted to be high, but which are lacking in collection records (fig. 3, table 2). Hotspots in the north-east of Kenya and in southern and west-central Tanzania have been poorly collected, despite several *Acacia* observations from these areas in the literature (Dharani 2006). Ground-truthing could verify predicted range extensions (table 1, electronic appendix 2) and improve parameterisation of temperature as a limiting factor for species such as *A. turnbulliana*.

Biodiversity assessments are highly dependent on the data available, thus affecting conservation prioritisation (Platts et al. 2010, Ahrends et al. 2011). Here, for example, some *Acacia* hotspots vary according to the subset of taxa considered: north-east Kenya in particular is more clearly emphasised by the subset of 36 taxa, which includes predictions of minor range extension, than by the set of 16 (excellent fit to known

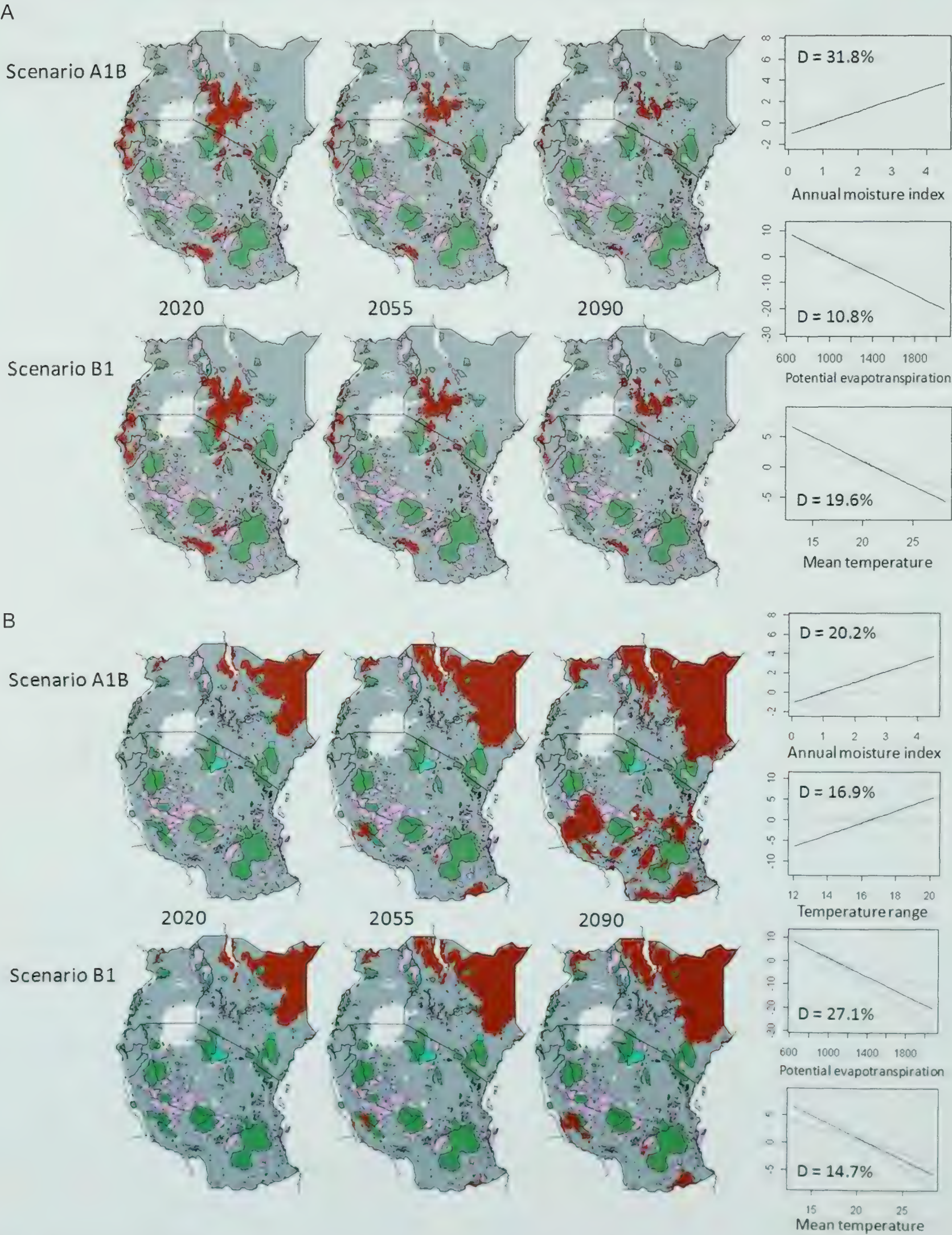


Figure 4 – Future range predictions for: A, *Acacia abyssinica* subsp. *calophylla*, and B, *Acacia turnbulliana* in relation to protected areas in East Africa. Red areas indicate predicted presence based on climatic suitability. Protected areas are shown in green (IUCN Ia-IV excluding Forest Reserves), blue (IUCN VI and Forest Reserves II-VI) and pink (non IUCN). Surfaces were derived from present day distribution model response curves (as shown, $\pm$ s.e., including predictor contribution, D). Straight line responses indicate either a preference for climatic extremes, or undersampling towards range limits.

distributions only). This discrepancy corresponds to a gap in the collection record, which necessarily renders occurrence predictions in north-east Kenya ‘range extensions beyond-’ rather than ‘excellent fits to-’ known distributions.

Climate change

Our application of a regional climate model, as opposed to a coarser, native resolution global circulation model, for predicting species distributions in the inter-tropical convergence zone has great potential to assist conservation planning. While sensitivity analysis would benefit from consideration of additional model calibrations (e.g. Jones et al. 2004) and scenarios (IPCC 2007), our results nonetheless highlight the potential for contrasting responses within a particular genus. The different ecological requirements of our two focal taxa resulted in very different responses to climate change: xerophytic taxa such as *Acacia turnbulliana* may benefit initially, whereas montane taxa such as *A. abyssinica* subsp. *calophylla* are predicted to reduce in range and become more dependent on weaker protected areas (fig. 4A). As montane taxa track changing climatic conditions (particularly rising temperatures) up the elevational gradient, the available space decreases, competition for resources increases, and eventually some may become locally extinct (La Sorte & Jetz 2010). If the predicted reduction in climatic suitability for *A. abyssinica* subsp. *calophylla* causes a reduction in the range of this taxon by the projected 65–80% by 2090, it could qualify as Endangered under criterion A3 of the IUCN Red List ($\geq 50\%$ population reduction projected or suspected over three generations, up to a maximum of 100 years; IUCN 2001). High elevation specialists may therefore be the group most threatened by rising global temperatures (Laurance et al. 2011), except in cases where complex topography provides climatic refugia – pockets of climatic stability undetected at the landscape scale (Austin & Van Niel 2011).

The behaviour of taxa in relation to both present and future climates is uncertain. For example, DMs rarely account for adaptability, dispersal or biotic interactions with competitors, food sources or predators (Guisan & Thuiller 2005). While the effects of climate change can be projected, direct human influences are more palpable. Habitat removal and overexploitation have been responsible for the inclusion of 80% of globally threatened species on the global Red List (IUCN 2011). Moreover, human influence has shaped the world’s ecosystems through a complex interaction with biotic factors (Hoekstra et al. 2005, Ellis & Ramankutty 2008). Conversely, *Acacia* distribution in Turkana (Kenya) has been shown to be more closely related to rainfall and elevation gradients than to long-term anthropogenic disturbances (Coughenour & Ellis 1993). Hence, while incorporation of land-use into DM outputs will help to improve accuracy, climatic and topographic factors will likely remain central to estimates of both current and future *Acacia* diversity.

Policy implications

Continued human pressure on habitats and species has led to the incorporation of biodiversity as the central theme of management planning of protected areas in East Africa. All five East African countries have ratified the Convention on

Biological Diversity (1992) and were party to the new Convention on Biodiversity Strategic Plan (2011–2020; UNEP 2010), which includes a commitment to achieve at least 15% coverage of “... comprehensive, ecologically representative and well-connected systems of effectively managed protected areas...”. Recent protected area designations based on biodiversity importance demonstrate this commitment in practice in East Africa (Davenport 2002, Marshall et al. 2007).

The question for managers is how best to deal with the potential mismatch between biodiversity and the current protected area network, both now and in the future. The strongest and most effective means of biodiversity conservation has consistently resided in the establishment of protected areas (Lockwood et al. 2006). In the future, this strategy could be strengthened by designating corridors as “stepping-stones” for wildlife between the existing fixed network designs. Repositioning of protected areas is out of the question due to the inherent uncertainties of both DMs and climate forecasts (Hunter et al. 2010), not to mention cultural, logistical and financial considerations.

Small-scale community initiatives underway in East Africa aim to encourage sustainable use of natural resources and the conservation of biodiversity-rich areas, including north-eastern Kenya. New conservation efforts do not necessarily have to follow the traditional format of protected areas and should work closely with local people, but ultimately must be based on solid science underpinned by verifiable and consistently collected data. Previous studies in the region have demonstrated the need for lower-level protected areas, such as forest reserves, to augment the biodiversity conserved by national parks and nature reserves (Burgess et al. 2007, Gardner et al. 2007). Our future range projection for a montane specialist emphasises the importance of high elevation climate refuges, where forest reserves are the most common form of protected area. While we emphasise that approximately half of the *Acacia* range predictions that are within protected areas correspond to levels of protection not recognised on the IUCN scale of I–VI, these sites do at least offer some legislated protection that may be built upon in the future.

SUPPLEMENTARY DATA

Supplementary data are available in pdf format at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consists of the following: (1) further details on analytical methods; (2) modelled climatic suitability for taxa in the genus *Acacia*; (3) envelope distance maps for climate variables used to model taxa in the genus *Acacia* for the present day and future IPCC-AR4 scenarios A1B and B1; (4) range predictions for *Acacia* taxa in relation to protected areas in East Africa; and (5) predicted impacts of climate change on climate suitability for *Acacia abyssinica* subsp. *calophylla*, and *Acacia turnbulliana*.

ACKNOWLEDGEMENTS

This work was funded by a Liz Claiborne Art Ortenberg Foundation grant to RG, RM and ARM. Funding from the

Udzungwa Forest Project, Flamingo Land Theme Park and Zoo, Marie-Curie (MEXT-CT-2004–517098) and The Leverhulme Trust (UK) is also gratefully acknowledged. Thanks to the Borderlands team (Walter Jetz, Daniel Kissling, Lucy Waruingi, David Western and Jeff Worden). We thank two anonymous reviewers, Pete Lowry and Elmar Robbrecht for their constructive comments on the manuscript. We thank the following institutions for assistance with data: National Herbarium of Tanzania; University of Dar es Salaam Herbarium; Royal Botanic Gardens, Kew; Missouri Botanical Garden; East African Herbarium/NMK; David Hassle; Phillip Omondi (ICPAC / Kenya Meteorological Office). We are grateful to Dr. Stefan Hagemann, Max Planck Institute for Meteorology for supplying REMO output. Thanks to Najma Dharani for commenting on model outputs. We also thank Najma and Random House Struik (Pty) Ltd for permission to use previously published figures. Thanks to Dave Hay and Colin McClean (University of York) for technical input. Thanks to all field assistants, especially Cara Reece, Liz Baker, Liz de Leyser, and the children of Luganga School.

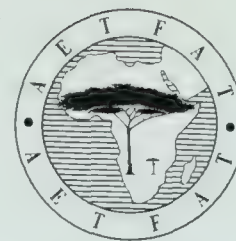
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Manuscript received 8 Nov. 2010; accepted in revised version 1 Mar. 2012. This paper was pre-published on 1 Nov. 2012 in issue 145(3) of *Plant Ecology and Evolution*.

Communicating Editor: Porter P. Lowry II.



The applicability of Relative Floristic Resemblance to evaluate the conservation value of protected areas

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Aims – It is important to know the contribution of a protected area to global conservation. A new method called ‘Relative Floristic Resemblance’ that uses databased and georeferenced herbarium specimens, is introduced. Its usefulness and applicability to assess the conservation value of protected areas is addressed.

Method – This is tested using the collection database of the National Herbarium of The Netherlands (NHN) and species checklists of Gabon and of five national parks in Gabon and the Central African Republic.

Results – The method proved to be a valuable instrument for revealing this conservation value, and can even, though with caution, be used for areas where a species list is still incomplete. We conclude that the four Gabonese parks are well chosen and each clearly conserve a different and comparatively unique flora. The Dzanga-Sangha Reserve captures a flora that ranges across a considerable part of the Congo Basin.

Key words – Conservation, protected areas, Relative Floristic Resemblance, biodiversity, flora, collection database, Gabon, Central African Republic, Dzanga-Sangha.

INTRODUCTION

Previously, national parks and other protected areas in Africa were generally created to conserve the fauna in these places, or to put it more bluntly, only large mammals mattered. The last decade, however, has shown a growing importance of the botanical composition and floral values when new protected areas are being created or existing ones are evaluated or extended. In many cases (e.g. Jansen et al. 1983, Jongkind 2010) simple species lists are being produced, and the interesting species discussed, in order to ‘evaluate’ conservation importance of the flora. In other studies a combination of criteria, such as number of endemics or rare species and different habitat types, is used to evaluate and/or select sites for conservation (e.g. Doumenge et al. 2003, Sosef et al. 2004).

However, it is also necessary to evaluate the value of a protected area by addressing its contribution to regional or global conservation (Gardner et al. 2007). To do this, one not only needs to know which species occur within such an area, but also where else these species occur. This is because we want to know how unique the species composition is on a regional or even global scale. A species that is endemic to a national park can only be conserved *in situ* in that park, and thus it gives the park a much higher status than a species with a broad distribution. For this reason some biodiversity assessment studies (e.g. Wieringa & Poorter 2004, Küper et al. 2004) weigh rarity. So, an area with a flora (and/or fauna)

that is comparatively unique, hence does not occur in other places, should receive high conservation priority.

Another element that may play a role when prioritizing areas for conservation is to what extent a protected area can vouch for other, unprotected areas. If a non-protected area has a flora that is also present in a protected area, the need to protect this area as well is reduced (at least from the botanical species-level viewpoint; of course there are plenty of other reasons to conserve such areas), and conservation efforts can better be focussed on areas whose flora is not yet secured.

These additional considerations for conservation planning cause a major problem for most conservationists, at least when they are not solely interested in well-known groups like large mammals or birds. For plants, for example, they might have performed inventories and have an idea about what occurs in the areas they want to assess, but they will generally not have information about where else these plant species occur and hence what the global importance of these areas is. In areas like tropical Africa, where the amount of available data on plant distributions is usually quite limited, such problems seem even more acute.

‘Relative Floristic Resemblance’, a method that uses databased herbarium records, may fill in this gap. This method has been tested using four recently established national parks in Gabon and one in the Central African Republic. These are: Batéké Plateaux N.P., Crystal Mountains N.P., Loango N.P. and Minkébé N.P. in Gabon (see fig. 1) and the Dzanga-San-

gha Reserve in the Central African Republic. These five parks were chosen because their flora is reasonably well known; the availability of a fairly complete species list is a prerequisite for this method. Moreover, the four Gabonese parks were only created in 2002, they have previously not been assessed for their floristic conservation value, and they are situated in four different corners of Gabon. Finally, we expected at least one of the four Gabonese parks (Crystal Mountains) to have a comparatively unique flora (based on the concept of rain forest refuges, see Sosef 1996), another two (Loango and Batéké Plateau) to harbour important savannah vegetations, while the fourth (Minkébé) together with the one in the Central African Republic (Dzanga-Sangha Reserve) are expected to contain more widespread species. Hence, we hoped these examples would be suitable to show various aspects of this new method. As a further demonstration of the method and aid to interpret the results, the analysis was also performed using the species list of the country Gabon as a whole.

Most of the surface of Gabon (80%) is covered by low-land tropical rain forest, the remainder being mostly savannah. Its highest mountains reach just over 1000 m. It is a centre of high biodiversity for African rainforest vegetation (Breteler 1990, Küper et al. 2004, Sosef et al. 2006) where many groups of forest taxa reach their highest species richness (e.g. Wieringa 1999, Versteegh & Sosef 2007, Breteler & Nguema Miyono 2008, Breteler & Wieringa 2008, Breteler 2010, 2011), rendering an analysis of Gabonese parks both urgent and interesting.

METHOD

To create species lists for four national parks in Gabon and the whole of Gabon the current Gabon-database (Sosef et al. 2006) was used. This is a subset of the collection database of the National Herbarium of The Netherlands (NCB Naturalis, section NHN) stored in the software package Brahms (Filer 2010) and can be consulted on the internet (<http://dps.plants.ox.ac.uk/bol/Gabon>). The NHN database now encompasses over 1.1 million collections records, of which about 340,000 relate to African specimens and 83% of these are geo-referenced. Of the over 74,000 Gabon records 98% are geo-referenced. Figure 1 shows the current collection density in Gabon as registered in the database. The species lists of all four parks are based on all geo-referenced specimens of vascular plants present in the database that are identified at least to species level and where the coordinates fall within the park or within a 10 km wide buffer zone around the park (table 1). Specimen selection was performed using ArcView GIS 3.3. For the Dzanga-Sangha Reserve in the Central African Republic a species list was provided in 2009 by David Harris (an update of Harris 2002). All analyses are conducted at species level. To achieve this, all six species lists (five parks plus Gabon) were extended to include all subspecific taxa, except those that are linked as synonyms to other names in the database. The extension was performed using the “Extend tags to all related infra taxa” tool in Brahms, subsequently all tags of synonym taxa were removed again.

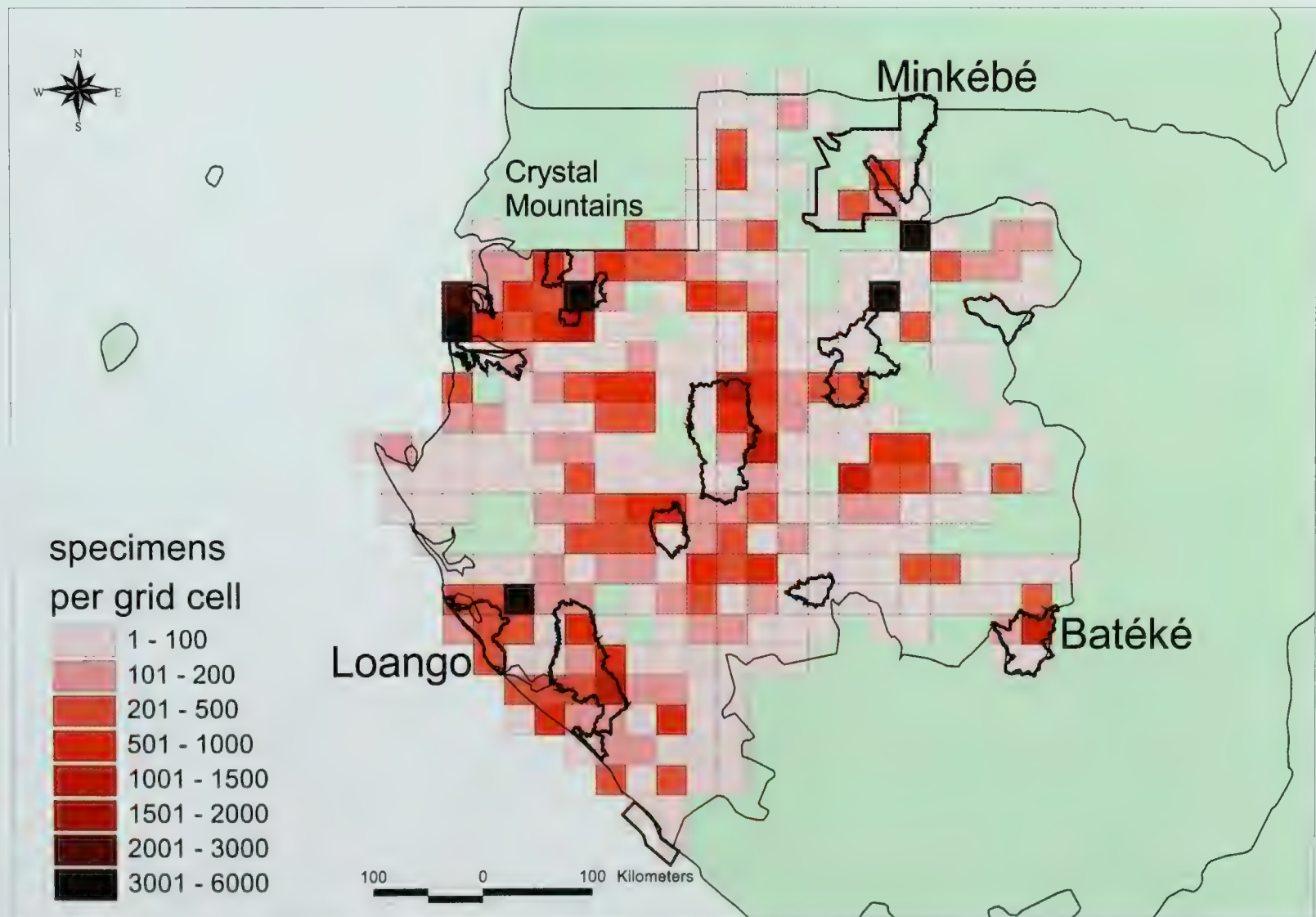


Figure 1 – Collection density in Gabon per $15^\circ \times 15^\circ$ grid cell. The boundaries of the national parks are shown by black lines. The four parks used in the analysis are provided with their short name. Crystal Mountains N.P. consists of two separate areas.

Table 1 – Number of collections and resulting species number for each National Park and for Gabon.

Collections are only considered if identified to at least species level and from within a 10 km radius of the Park. For the Gabon list all identified records from Gabon have been used.

locality	collections	species
Batéké	861	473
Crystal Mountains	4223	1351
Loanga	1418	782
Minkébé	1099	609
Dzanga-Sangha	c. 5600	1012
Gabon	57713	5197

Using all geo-referenced and fully identified records of vascular plants present in the NHN collection database, a grid cell table covering the whole world containing the number of species in each cell was obtained. Similar tables were prepared counting only the species present in the six species lists. These tables were prepared with Brahms 6.7 (Filer 2010) using the DistDiv procedure on species $\times$ grid cell with options “exclude cultivated botanical records”, “always use accepted name” and “exclude vague name” on. The species only present in the six species lists were counted for each grid cell by first extracting all collection records of species from these lists (including synonyms) and then running the DistDiv procedure using the option “extracted botanical records only”.

We have defined the ‘Relative Floristic Resemblance’ (RFR) of a cell to a specific area (e.g. National Park or country) as the proportion (expressed as a percentage) of species present in a cell that also figure in the species list of that area. Thus, to obtain the RFR of each grid cell to each park and to Gabon the number of species in each cell that are present in the reference area list was divided by the total number of species for that cell, and expressed as a percentage. Grid cells that are completely covered by the reference area of course always result in a RFR of 100% (see e.g. fig. 2). To evaluate the extent of national park floras over Africa, the grid cells size was set to $1 \times 1^\circ$. For a more detailed analysis within the

Lower Guinean floristic region, cells of $15 \times 15'$ (c. 28×28 km) were used.

Only cells with more than ten known species are considered in this analysis. The results are visualized in grid cell maps. But, since not all grid cells in Africa reach this number, and some zones are quite empty because of lack of data in the NHN database (e.g. Sahara, Botswana), the image is sometimes too scattered to be read easily. Therefore, interpolated maps have also been created. Interpolation was performed in ArcView using interpolating method IDW, twelve neighbours, second power, and no barriers.

RESULTS AND DISCUSSION

The wetter zones of tropical Africa are roughly divided into four phytogeographical regions, three are part of the Guineo-Congolian regional centre of endemism: Upper Guinea (Liberia to Togo), Lower Guinea (southern Nigeria to northern Angola) and Congolia (most of the Republic of Congo and D.R.Congo), where the fourth is formed by some isolated forest patches in the Zanzibar-Inhambane regional mosaic (White 1979, 1983). The RFR maps of Gabon (fig. 2) show a high resemblance of the flora of both Lower Guinea and Congolia to that of Gabon, much stronger than to that of Upper Guinea. In the latter area the highest resemblance is found in the SE corner of Liberia which is the wettest part of West Africa. The more detailed $15 \times 15'$ grid cell map shows that the vegetation in the whole of Equatorial Guinea and southern Cameroon resembles the Gabonese flora to a very high degree, except in the mountainous areas of West Cameroon and Bioko which harbour a mountain flora not present in Gabon. This also shows how to read the maps: the resemblance of a grid cell to the ‘source area’ only shows which proportion of the species in that cell also occurs in the checklist area (in this case Gabon). It does not show how many Gabonese species are not found in that grid cell, nor if this grid cell is relatively rich or poor in species. So, it only tells you what percentage of the flora of the grid cell is ‘covered’ by the flora of Gabon; hence what proportion of its species are conserved if the whole of Gabon was a protected area.

The species lists for the five national parks (table 1) show an enormous difference in species numbers. Crystal Mountains is by far the richest park with 1351 species, followed

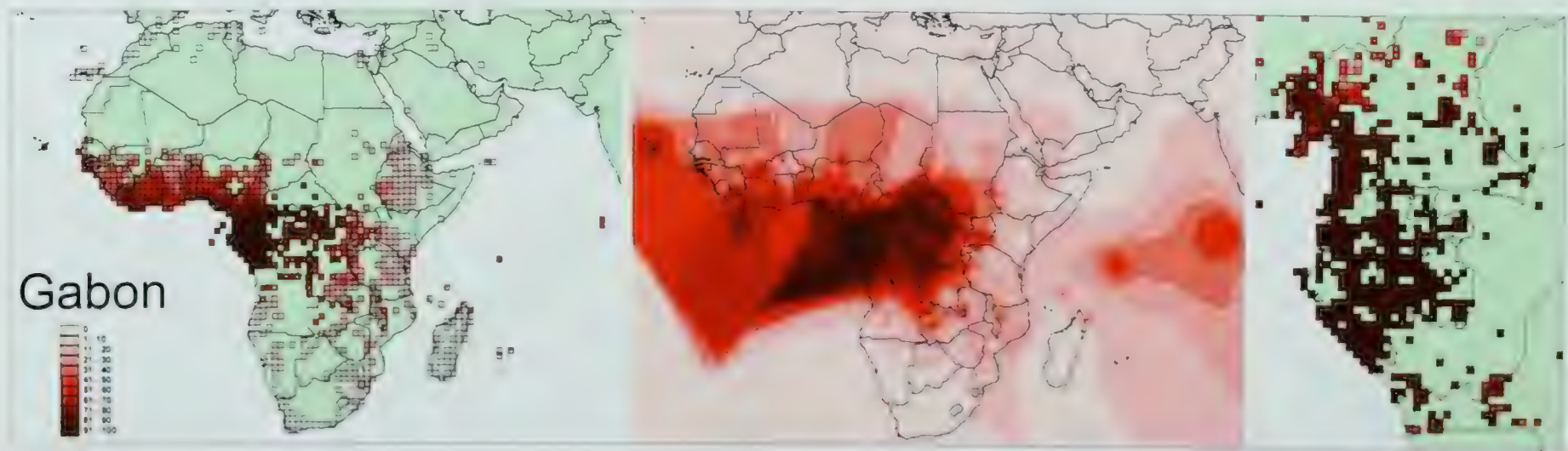


Figure 2 Relative Floristic Resemblance map for the flora of Gabon, on the left using grid cells of $1 \times 1^\circ$ (only showing grid cells with more than ten known species), in the centre the interpolated map for $1 \times 1^\circ$, and at the right a map zooming in on Lower Guinea using grid cells of $15' \times 15'$. The national parks are indicated by their boundaries.

by Dzanga-Sangha (1012), Loango (782) and Minkébé (609). Batéké Plateau has the lowest species number with only 473 species. Both Batéké Plateau and Minkébé are presumably richer than is shown by these numbers because for both parks some botanical collections have not yet been included in the NHN database and in both only a very limited part has been explored botanically. A provisional species list for Batéké Plateau (Walters 2007) that includes many non-vouchered records already shows slightly more names (522, but only 461 identified to species level) while there have been many new identifications since. The species lists for Batéké Plateau and Minkébé can thus be used in this study to evaluate the effect of incomplete species lists.

The maps showing the results of the RFR analyses for the five parks (fig. 3) show quite different pictures. Some parks like Loango and Batéké Plateau have a flora that apparently is quite unique and hardly extends outside of these parks. Other parks like Crystal Mountains and Dzanga-Sangha have a high resemblance over vast areas of central Africa. Strikingly enough, these last two parks do not show a lot of overlap in resemblance area; they are quite complementary to one another. Although it does not have the largest species number, the Dzanga-Sangha reserve does show the largest area with a high resemblance in Africa. We may thus conclude that thanks to the protection of the Dzanga-Sangha reserve, a fair portion of the flora of the entire Congo Basin has been secured, at least at species level. In the 1° grid cell analysis the cells of the Minkébé N.P. show a fairly high resemblance to Dzanga-Sangha. However, in the more detailed analysis the RFR's are not that high, and although Minkébé shares a lot of species with Dzanga-Sangha, Minkébé apparently also has a set of locally more common species (represented in several 15' cells) that it does not share. Since we know that the Minkébé inventory has a strong emphasis on woody plants, especially large trees, this may well be the cause of this effect. This is corroborated by the result that the more western grid cell in the park, where the sampled flora is based on the last part of the A-transect (van Valkenburg et al. 1998) and hence consists solely of large trees, has a lower resemblance to Dzanga-Sangha than the two cells along the Nsing River, where general collecting also took place. This apparent effect, that large trees show more local diversity patterns than plant species in general, should be analysed in further studies.

Of the four assessed Gabonese parks only Crystal Mountains has an enormous species count and the conservation effect extends over a large area. However, all eleven other terrestrial national park grid cells show only between 25 and 67% resemblance to this park, meaning all these parks still harbour quite a lot of species not present in Crystal Mountains N.P. and hence none of these parks becomes superfluous. The same is true for the other three Gabonese parks that were assessed: none of the other parks show a lot of resemblance to any of these three parks, and it thus seems the park areas have been very well chosen. The parks that have a flora with a very limited extent (Loango and Batéké) not only show very low resemblance from other parts of Gabon, but these parks likewise show less resemblance to other parks (like Crystal Mountains). This combination points to the unique flora these two national parks harbour. Although both parks have a large savannah component, their floras do not resemble each

other either. This conclusion is corroborated by the study of Walters et al. (submitted); the flora of Loango is discussed in more detail by Harris et al. (submitted). For Batéké Plateau it is striking that it has a much higher correlation with some parts of Congo-Kinshasa than with nearby Gabonese cells. Since most of the park soil consists of Kalahari sands, Walters et al. (2005) expected a relative high correlation with other areas with Kalahari sands like eastern Angola. But since no grid cells in eastern Angola reach eleven species, we do not have any data points to corroborate that hypothesis.

As stated above, the species lists for Batéké Plateau and Minkébé are relatively incomplete. Incomplete species lists will have the effect that a grid cell may have some species that will be scored as "not occurring in the reference area", while in fact they do occur there. This results in lower resemblance values. However, one may expect the effect to be equal for all cells; for example if 32% of the real number of species in a park is not yet on its species list, the RFR values will also, on average, be 32% lower. So, in theory, the map for that park will show a paler image than if a complete list were available. Indeed fig. 3 shows us that the maps for these two parks are in general paler than the other maps. However, the image that starts emerging for e.g. Minkébé is as was expected for this park: high affinities with south-eastern Cameroon, northern Congo-Brazzaville and parts of the Congo Basin. That the overall image does appear (though paler) proves that the method can be used for parks with a partially incomplete species list. But, judgements regarding the uniqueness of their flora should be made with extreme caution. A second effect, however, will be that this error will introduce its own variation by chance, on top of the variation introduced by the subset of known species for a grid cell, resulting in 'spotty' maps. Both types of variation will be smaller if the number of known species of a grid cell is larger. The interpolated maps for Batéké Plateau and Minkébé indeed show a spotty image, especially in the Congo Basin, an area where in our database the number of collections per grid cell is usually quite low. On the other hand this does not yet disturb the overall impression obtained about the resemblance patterns for these parks. If the increased variation is judged to be too disturbing, it is possible to set the minimum number of species in a grid cell to fifteen or twenty instead of eleven as was used here. Where to place this cut-off value will always be a compromise between getting results from more grid cells against possibly getting some grid cells with extreme results caused by random variation in cells with few data. Therefore, the 'ideal' cut-off point will tend to be higher for analyses of parks with incomplete species lists.

An interesting effect that can be observed in the resemblance maps of Gabon is that some low altitude, isolated oceanic islands like the Seychelles, the Maldives and Cape Verde show a higher resemblance than other areas at the same distance (best shown in the interpolation where the sea is coloured to show what would have been expected if it were land). These low oceanic islands usually have a relatively poor flora with few endemics and comparatively high numbers of pan-tropical weeds and beach species. So, due to this their flora concurs for a fair part with the Gabonese flora. Most national park analyses do not show this effect, pointing to a low number of pan-tropical weeds collected in these

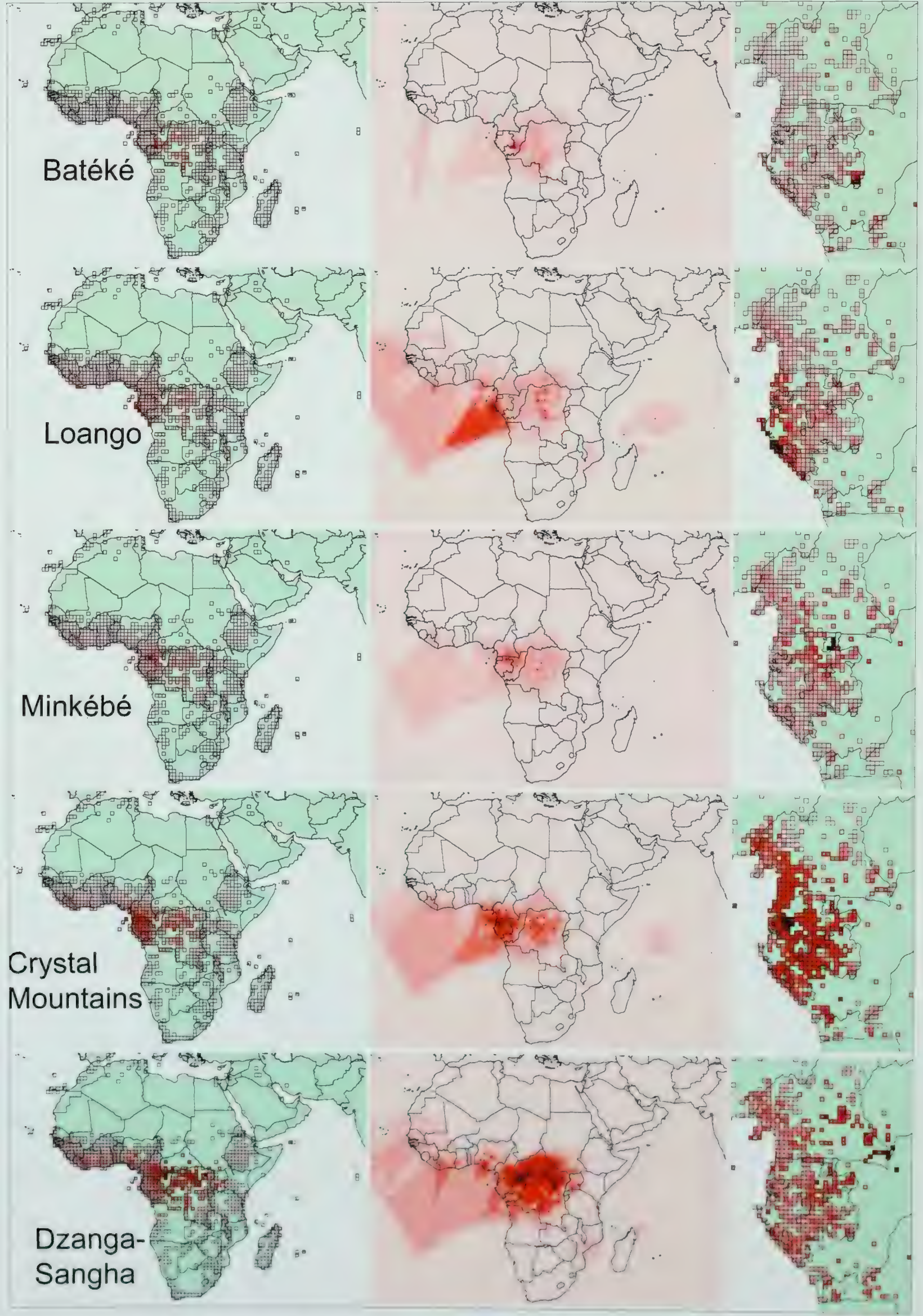


Figure 3— Relative Floristic Resemblance maps for the protected areas Batéké Plateau, Loango, Minkébé, Crystal Mountains and Dzanga-Sangha. From left to right as in fig. 2.

parks. The only exception is the coastal park Loango that does show elevated values in all these islands. Upon closer examination, the common elements indeed prove to be some weeds and pan-tropical grasses.

Relative Floristic Resemblance can also be used to evaluate which parts of a region or country have a flora that is not yet protected by the present park system. If Gabon were to have such areas, they should be considered for conservation. However, such an analysis, where we can assess which part of the Gabonese flora has not been covered for by the present park system, can only be performed if fairly complete species lists are available for all of the present parks, and this is not yet the case. At the moment there is even one park (Mwagne) where not a single plant species is known from within its borders, and quite a number of parks where very few collections are known (e.g. Birougou) or only a small part of the park has been visited by botanists (Minkébé, Batéké Plateau, Pongara and Ivindo). Although such a combined analysis would be most welcome, at present it cannot be properly performed and more inventory work in the above mentioned parks, as well as to yet uncollected areas in Gabon, is needed.

CONCLUSIONS

'Relative Floristic Resemblance' using digitized and georeferenced herbarium specimen data proves a powerful and useful tool to assess the botanical conservation value and extent of protected areas. This method works well if the total plant species content of the protected area is fairly well known. For protected areas where the included species are only partly known, the resulting map is paler (overall lower resemblance) but the general resemblance pattern does appear. Users should be aware that in such cases the image is too pale and compensate for this prior to drawing conclusions. To avoid too much variation for some grid cells due to data artefacts, the user may increase the cut-off value for the minimal number of species per grid cell. This method does not need a lot of data for areas in the rest of the region addressed to work properly. Occurrence data of fifteen to twenty species per grid cell will be enough for analyses of incomplete species lists, while as few as ten may work for complete lists; for many areas often no more data than this is available, and for such areas this method will be the only one available. Grid cell size of an analysis will depend on the research question (local or more general) and the amount of available data.

The conservation value of the Dzanga-Sangha appears to extend well into the Congo Basin; hence, a considerable part of the Congo Basin forest flora is probably under protection thanks to this park.

The four Gabonese parks analysed appear to have very different and unique floras. These parks cannot vouch for any of the other terrestrial Gabonese parks. On the other hand, the flora of some parks is so poorly known that even their resemblance to well-known parks cannot be assessed. These parks urgently need to be inventoried. When all parks have fairly complete species lists, a combined analysis can be performed to assess which part of the Gabonese flora has not been covered by the present park system, and which areas need protection in order to overcome this shortcoming. This will prove

very useful advice to governmental agencies, NGO's and conservationists on where to plan or move future parks.

The power of this method may be improved substantially if all data available in collection databases of herbaria around the world is pooled (as is already the case for the Gabon database). Then more detailed 30' or 15' grid cell analyses can be performed over larger areas, and analyses performed for protected areas in countries where single herbaria databases hold insufficient data.

ACKNOWLEDGEMENTS

David Harris from Royal Botanic Garden Edinburgh provided an updated electronic version of the species list for the Dzanga-Sangha Reserve. Gretchen Walters from Missouri Botanical Gardens, St. Louis provided data to assess the completeness of the Batéké species list. Both helped to understand and interpret the results for these parks, and also that for Loango National Park. Laurent Gautier and two anonymous reviewers provided valuable comments for this paper, and Christina Flann kindly improved the English. This study was only possible thanks to the extensive geo-referenced collection database present in NCB Naturalis, section NHN. This database has been built over the past decades by dozens of people, painstakingly databasing or identifying plants. Major parts of it were built thanks to projects like ECOSYN (EU project B7-5041/95-02/VIII), NWO-Groot (project 175.010.2003.010 of The Netherlands Organization for Scientific Research) and Biodiversité Botanique du Gabon (Directorate General for International Cooperation (DGIS), the Netherlands, project GA 000 402). Moreover, the following herbaria made available their electronic data to be compiled into a single Gabon database: BR, BRLU, MO, P. We would like to thank Denis Filer from Oxford University for proving us with the DistDiv module in Brahm's that was used extensively in this study, and several tools that facilitate the extraction of species list including records stored under synonyms or subspecific names.

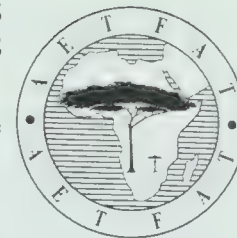
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Manuscript received 31 Oct. 2010; accepted in revised version 5 Aug. 2011. This paper was pre-published on 15 Nov. 2011 in issue 144(3) of *Plant Ecology and Evolution*.

Communicating Editor: Laurent Gautier.



Recovery of forest biodiversity by natural ecological processes through native or alien tree stands

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Background and aims – Each natural forest area has species that function optimally in different development stages of that forest system. In forest rehabilitation we often plant mature forest species and ignore those species with adaptations to recover effectively after severe disturbance and degradation, and produce useful products at a fast rate. We clear stands of invasive alien species before we plant native tree species, all at great costs, to rehabilitate natural forest. By contrast, cost-effective commercial plantation forestry systems generally use fast-growing pioneer tree species introduced from other natural forest regions, which often facilitate the recovery of shade-tolerant native forest species. This paper provides a brief overview of how pioneer tree stands in different natural forest systems in Africa and Madagascar develop from monocultures to diverse mature forest communities.

Methods – Three examples of natural forest pioneer tree stands are used to provide a brief overview of their development towards diverse mature forest: *Virgilia divaricata* after fire in South Africa, *Musanga cecropioides* after slash-and-burn agriculture in the Congo Basin, and *Ravenala madagascariensis* on the forest margin in southeastern Madagascar.

Key results – Mono-specific pioneer stands on sites of degraded or cleared forest develop through different recovery stages, each with its own suite of species, towards mature, mixed-species forest. Several recovering species are important commercial timber species which do not regenerate in mature forest.

Discussion – The results are compared with the parallel process of forest recovery through planted and naturalized species of invader trees (pines, eucalypts, acacias) and shrubs (*Chromolaena odorata*) as a basis for guidelines on rehabilitation of natural forest in an area.

Conclusion – The process of forest recovery through planted and naturalized invader and native pioneer stands can be managed to rehabilitate natural forest biodiversity, processes and productive capacity without alien plant clearing or planting of native tree species while providing a source of income and manipulating the invader plant species out of the system.

Key words – Diversity, ecotone, invasive alien plants, pioneers, timber plantations, succession.

INTRODUCTION

There are many projects to plant natural forest species to rehabilitate forest or to combat perceived deforestation such as through slash-and-burn agriculture, and people search for species to plant, often the wrong species for the specific site conditions. We often forget that each natural forest area has species that function optimally in different development stages of that forest system. Commercial forestry organizations plant useful, fast-growing, often natural pioneer tree species introduced from other natural forest regions, in appropriate systems to produce timber, poles, fuel wood, pulpwood, etc. cost-effectively. They have to consider the costs of silvicultural and fire protection actions. In the process

some of the species may become invasive because of their pioneer characteristics. By contrast, many natural forest rehabilitation efforts employ very costly systems in wrong sites with questionable success. In such efforts people plant a wide range of mature forest species in exposed sites and expect a quick recovery of the natural biodiversity (Knowles & Parrotta 1995, Parrotta et al. 1997a). They clear invasive alien species at great costs to plant native species also at great costs. They use elaborate and costly nursery and planting actions. Many such projects ignore those species specifically adapted to easily recover from severe disturbance and degradation, to facilitate natural biodiversity recovery, and to produce useful products at a fast rate. Generally resource

managers and ecologists have a poor understanding of the natural disturbance-recovery processes at the landscape level and how these relate to resource use practices, and forest recovery.

Many examples of degradation of natural forest exist. These include human disturbance activities of resource use, crop cultivation, mining, changed land uses (invasive alien plants, grazing, increased/decreased fire regimes). They also include natural disturbances by fire, lightning, cyclones or hurricanes, windfalls, flooding, drought, etc. When we take a closer look, we find many similarities and also major differences between natural and human impacts through such disturbances, and the recovery processes. For example, forest destruction by a fire in the natural evergreen forest caused by lightning, or flying sparks from an adjacent shrubland, looks very similar to the destruction of a forest caused by slash-and-burn agricultural practices (fig. 1B) in terms of destroying forest structure, removal of the vegetation cover, and vegetation recovery. The warm-temperate evergreen forest in the Bloukrans Pass area, South Africa, soon recovered through natural forest pioneer species after the lightning fire burnt there for two months (Geldenhuys et al. 1994). Slash-and-burn clearings in the same area shown in figure 1 also recovered to local pioneer tree species of *Musanga cecropioides* R.Br., *Harungana madagascariensis* Lam. ex Poir. and others (see fig. 6) before they get cleared again in the forest-cropping-fallow-forest conversion cycles (C.J. Geldenhuys, personal observation, 2007).

The fragmented forest distribution in many areas is often attributed to clearing by people but mostly this is not the case, although land use is a contributing factor to different degrees in different areas. The fire regime in particular determines forest-woodland-shrubland-grassland mosaics in the broader landscape where the annual rainfall intensity and seasonality is high enough to maintain natural evergreen forest (Geldenhuys 1994). In such areas the actual forest area is often a small to very small portion of the potential forest area in the landscape. It is important to understand this interaction between fire patterns in the landscape and forest location pattern because this provides an important basis for under-

standing how to manage the majority of invasive alien plant species in the natural forest environment.

South Africa, for example, has experienced a long period of fire ignition by lightning and people. The fires driven by prevailing winds in the dry season determine the forest location pattern because "hot air moves up and fire cannot climb down a cliff but jumps over the edge" (figs 2 & 3; Geldenhuys 1994). This movement of the air creates an eddy on the leeward side of a ridge. Fire sparks carried by the wind jumping across a ridge can start a spot fire which could run with an eddy up the ridge from the leeward side. Commercial timber plantations are generally planted in the fire pathway and require costly fire protection systems, but during extreme conditions some plantations get regularly destroyed by fire (fig. 4). This suggests that any forest rehabilitation activities within the fire zone will require costly fire protection actions. Natural forests persist in mountainous landscapes surrounded by fire-adapted grassland, shrubland and woodland in topographic shadow areas in relation to wind-driven fires in the dry season.

The degree of disturbance to a particular entity (individual, population, community, ecosystem or landscape) determines the rate of recovery of that entity. A specific disturbance event can be a non-event if it has a very minor impact on the entity, or an incorporated disturbance if the entity is adapted to the impacts of the disturbance, or a disaster if the entity has been transformed into a new state (Hansen & Walker 1985). For example, a tree-fall gap is a disaster to the specific tree(s), an incorporated disturbance for light-demanding species and the stand and a non-event for the forest. Different situations therefore require different approaches to find solutions towards forest/species recovery in disturbed forest.

Natural forests have intrinsic adaptations to recover from diverse disturbance regimes (fires, cyclones, landslides, volcanic eruptions, windfalls, etc.) through suites of species dominating stands in different development stages towards recovery to mature forest. The total forest biodiversity of a particular forest system is therefore a function of the habitat

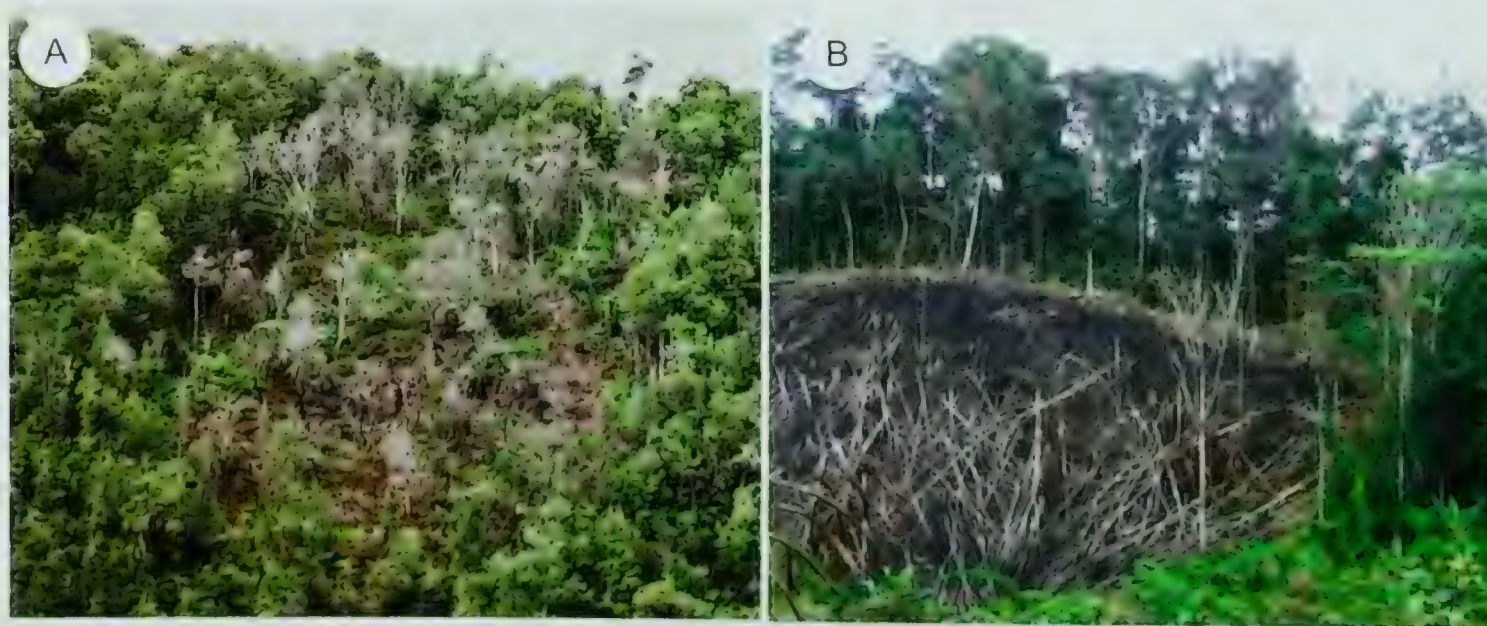


Figure 1 A, forest destruction by a lightning fire in Bloukrans Pass area, South Africa (Geldenhuys et al. 1994) compared to B, forest destruction caused by slash-and-burn clearing for crop cultivation in the Guietso area, southern Gabon (C.J. Geldenhuys, personal observation 2007).



Figure 2 – Fire flows (solid lines) along ridges, and jumps (dotted lines) across gullies to contribute to the fragmented forests location pattern within fynbos near Swellendam (A) and within grassland in the Cathedral Peak area, KwaZulu-Natal Drakensberg (B & C), South Africa.

and the suite of recovery stages after diverse disturbances. Different species in such a forest system function optimally in different development stages to mature forest, such as pioneer species in disturbed sites to shade-tolerant species in mature forest, and they require such conditions to maintain healthy populations. Our challenge is to recover the biodiversity and productivity of degraded or cleared natural forests cost-effectively.

The concept of this paper is that in the forest environment many invasive alien plant species are nothing more than pioneer species that facilitate the forest recovery process when the disturbances are removed from the system, similar to the local pioneer species. The objectives of this paper are (i) to provide a brief overview of the development of three types of pioneer tree stands towards mixed regrowth forest in different natural forest systems in Africa and Madagascar, (ii) to compare this development process with indigenous forest species establishing in stands of introduced commercial timber (and alien invasive) species of pines, eucalypts and acacias, and then (iii) to develop basic guidelines for conversion of invasive alien and natural pioneer stands towards recovery of diverse forest.

STUDY AREAS

Three examples of pioneer tree stands in natural forest systems are used here to provide a brief overview of their development from monocultures to diverse forest communities:

Virgilia divaricata after fire in Southern Cape Afrotropical forest margins

Virgilia divaricata Adamson (Asteraceae) is an endemic, fire-adapted legume pioneer tree along the margins of the Southern Cape Afrotropical forests particularly the mountain forests (Phillips 1926, Geldenhuys 1993, 1996a). The species develop soil-stored seed banks which have been estimated to be at least 230 years old with still viable seeds (Geldenhuys 1994, Geldenhuys et al. 2003). The seed needs hot fires to germinate in mass (with some scorched to death), as can be seen from the example of a fire that burnt into Klein Witelsbos in the southern Cape (fig. 5A–C; Geldenhuys et al. 2003). The initial dense pioneer stands contained no seedlings of other forest species. Such stands grow rapidly to a height of 4–6 m and undergo rapid self-thinning with a gradual decreased stand density and more growing space developing in the understorey, allowing other forest species to become established (fig. 5D).

Musanga cecropioides in slash-and-burn sites in tropical moist forest, Gabon

Musanga cecropioides R.Br. (Parasolier; Cecropiaceae) is a large-leaved typical forest pioneer tree in disturbed and cleared tropical moist forest in the Congo Basin and West Africa. It is the main pioneer species in the abandoned sites of slash-and-burn agriculture. Tropical moist forest tree species recover in such pioneer stands. In Gabon the main com-

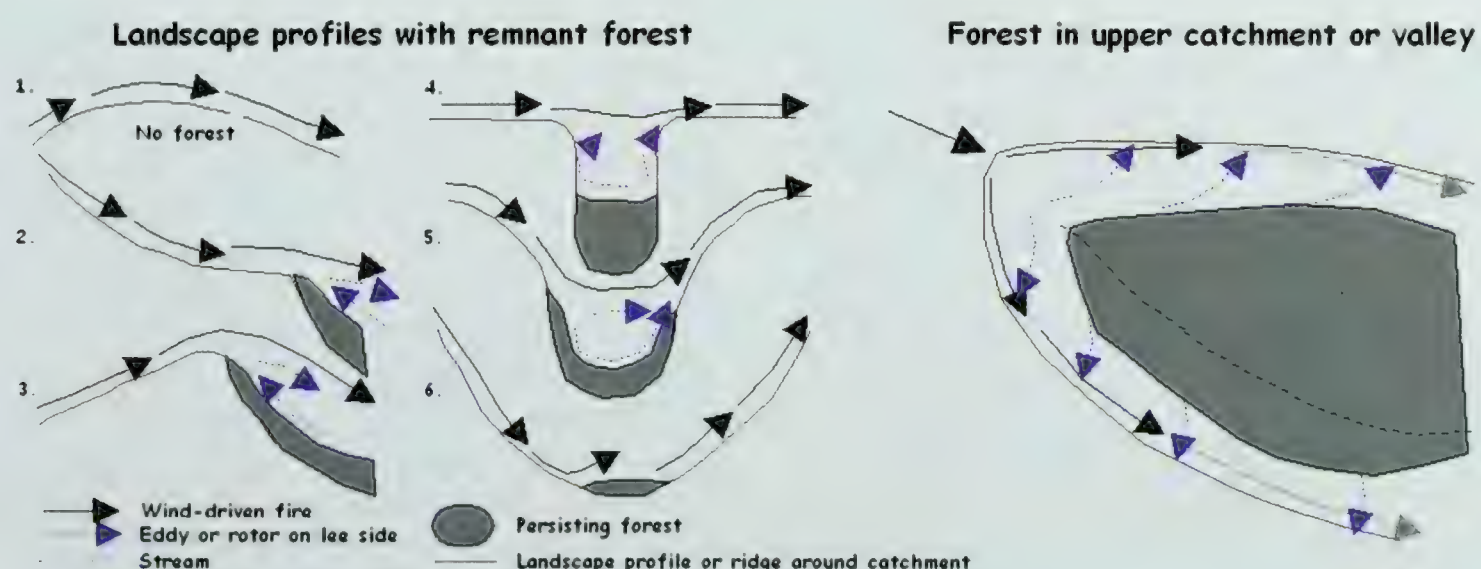


Figure 3 – Generalized model of forest location pattern in fire shadow areas with fire-adapted fynbos shrubland or grassland in the fire pathways within broken landscapes (adapted from Geldenhuys 1994).



Figure 4 – Commercial timber plantations planted in grassland/fynbos within the fire zone were destroyed by severe wild fires while the natural forests were not destroyed at all, at Langverwacht plantation near Kokstad (A) and Witelsbos plantation near Humansdorp (B) in South Africa.



Figure 5 – Stages in the development of *Virgilia divaricata* pioneer stands after fires in the Southern Cape: A, mass regeneration from soil-stored seed bank under the burnt Klein Witelsbos forest canopy after a fire in June 1996; B, the pioneer stand after 4 months and C, after 11 months; D, mature forest species of *Ocotea bullata*, *Curtisia dentata* and *Rapanea melanophloeos* under a advanced developed *V. divaricata* stand (unknown age) in Gouna.

mercial timber tree *Aucoumea klaineana* Pierre and other commercial timber species regenerate along with such pioneer stands. Figure 6 shows the process of clearing a forest for growing crops such as manioc, sugar cane, maize, banana and other crops. After 2–3 years the crop fields are overgrown by *M. cecropioides*. Some stands get cleared again in the forest-cropping-fallow-forest conversion cycles together with the commercial timber species, but sometimes they do develop into regrowth forest.

***Ravenala madagascariensis* in Manombo Special Reserve, south-eastern Madagascar**

Ravenala madagascariensis Sonn. (Strelitziaceae) is a banana-like plant, low-growing or tree-like, with large long leaves, and it does form one or more woody branch-free stems similar to palm trees. *R. madagascariensis* is exten-

sively used in the construction of houses in the villages: the stem for the walls of the houses and the leaves for thatching the roofs. It is also fire resistant and rapidly recovers after fire and prevents grassland fires to enter the forest (fig. 7).

In the Farafangana-Manombo area *R. madagascariensis* is common in three types of habitats (Anonymous 1996): (i) Inland at 10–30 km from the coast they occupy the forest margin, maybe with *Trema orientalis* (L.) Blume, on the bauxite rocky ridges along a topographical gradient between the grassland-*Strychnos spinosa* savanna transition zone (with a variety of stems of the invasive alien *Psidium guyava* L. and *Lantana camara* L. and a variety of herbaceous species) on the side of the fire-affected landscape, and the primary forest on the leeward side of the ridge (fig. 8); (ii) within the coastal forest on sand, in frequently inundated depressions, swamp forest is dominated by mainly two species, *R.*



Figure 6 – The forest-cropping-fallow-forest conversion cycle in tropical moist forest in southern Gabon: A, mature tropical moist before it had been cleared for growing crops; B, Parasolier (*Musanga cecropioides*) regrowth stand of about 15 years (middle back) that is cleared for crops (front) together with some timber species, including Okoume (*Aucoumea klaineana*); C, young Parasolier over-taking planted banana to develop into D, a proper young pioneer Parasolier stand; E, Okoume stand which developed through the Parasolier pioneer stand in a site where ground nuts were cultivated about 35–40 years before (local knowledge).



Figure 7 – *Ravenala madagascariensis* (B) forms a buffer between A, grassland fires and the forest and C, between the resource use needs of the villagers for house construction (roof and walls) and the forest.

madagascariensis and *Anthostema madagascariensis* Baill., either mixed stands of the two species or in the form of contiguous mono-specific stands. *R. madagascariensis* reaches 15 m height and *A. madagascariensis* reaches 12 m height and stems of 25 cm DBH. In the marshes in the same area *R. madagascariensis* has shorter stems (4–5 m) than in the swamp forest; (iii) the species is also present in the savoka (regrowth of forest on abandoned land) of former slash-and-burn (tavy) sites. Pioneer species such as *Harungana madagascariensis* and *R. madagascariensis* dominate and may include *Trema orientalis* and *Strychnos madagascariensis* Poir. Some fire-tolerant species from the primary forest can develop in the savoka, mainly the genera *Dombeya*, *Tambourissa*, *Ficus*, *Homalium*, *Filicium* and *Cabucala* and are capable of resprouting after being cut in a tavy. Some mature forest trees are not cut down during a tavy such as trees of

Humbertia madagascariensis Lam. – their timber may be too hard and they persist in the landscape.

METHODOLOGY

Virgilia divaricata on Southern Cape Afrotropical forest margins

In a study to classify and describe the Southern Cape Afrotropical forests, 250 circular 0.04 ha plots were sampled along six belts from the mountains to the coast to cover the main environmental gradients in the Southern Cape Afrotropical forests (Geldenhuys 1993). Tree data included all stems ≥ 5 cm stem diameter at breast height (DBH). This data set was searched for plots containing *V. divaricata* plants of all sizes (including dead stems) to assess the development of other forest species within the pioneer stands of

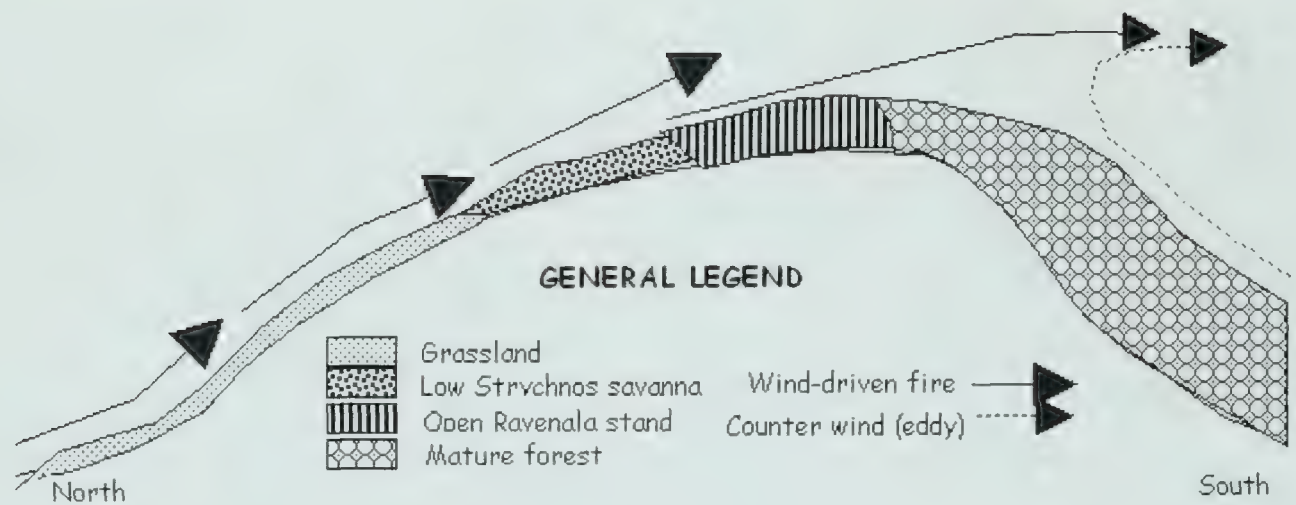


Figure 8 – The position of *Ravenala madagascariensis* between the primary forest and the grassland-*Stychnos spinosa* savanna on the northern forest edge in the Manombo Special Reserve forests on the inland low ridges, Madagascar (Anonymous 1996).

Table 1 – Composition of mature forest species on six 0.04 ha plots sampled in developing *Virgilia divaricata* stands after succession from a starting point of pure pioneer *V. divaricata* stands (fig. 5), Southern Cape Afrotemperate Forest, South Africa. After *V. divaricata*, species are arranged by stem density.
* Species with non-fleshy fruit; +Introduced invasive species

Species	% of plots	Stems /ha	Basal area m ² /ha
<i>Virgilia divaricata</i> Adamson	66.7	68.8	1.84
<i>Cunonia capensis</i> L.*	66.7	291.7	13.14
<i>Ocotea bullata</i> (Burch.) Baill.	100.0	220.8	12.17
<i>Podocarpus latfolius</i> (Thunb.) R.Br. ex Mirb	83.3	162.5	2.96
<i>Gonioma kamassi</i> E.Mey.*	50.0	108.3	1.47
<i>Pterocelastrus tricuspidatus</i> (Lam.) Walp.	50.0	87.5	4.85
<i>Rapanea melanophloeos</i> (L.) Mez	66.7	66.7	0.45
<i>Brachylaena glabra</i> (L.f.) Druce*	16.7	50.0	1.64
<i>Pterocelastrus rostratus</i> (Thunb.) Walp.	16.7	50.0	0.50
<i>Podocarpus falcatus</i> (Thunb.) R.Br. ex Mirb	16.7	33.3	3.52
<i>Olea capensis</i> L. subsp. <i>macrocarpa</i> (C.H.Wright) I.Verd.	33.3	25.0	0.96
<i>Platylophus trifolius</i> (L.f.) D.Don*	16.7	25.0	1.32
<i>Halleria lucida</i> L.	50.0	20.8	0.09
<i>Ilex mitis</i> (L.) Radlk.	16.7	16.7	0.62
<i>Olinia ventosa</i> (L.) Cufod.	16.7	12.5	2.50
<i>Diospyros glabra</i> (L.) De Winter	16.7	8.3	0.03
<i>Curtisia dentata</i> (Burm.f.) C.A.Sm.	16.7	8.3	0.32
<i>Canthium inerme</i> (L.f.) Kuntze	16.7	8.3	0.02
<i>Chionanthus peglerae</i> (C.H.Wright) Stearn	16.7	4.2	0.01
<i>Robsonodendron cuculiforme</i> (Fekl. & Zeyh.) R.H.Archer	16.7	4.2	0.02
<i>Acacia melanoxylon</i> R.Br.+	16.7	4.2	1.46
Mean stand values		1254.2	49.28

V. divaricata. Six plots containing *V. divaricata* trees were found: one in Jonkersberg area, two in Groenkop area, two in Witelsbos area and one in Kromrivier area. Two selected plots had no live trees of *V. divaricata* (only some dead stems either leaning onto other trees or lying on the forest floor, as seen in the other four plots). The younger pure stands of *V. divaricata* are represented by the pictures in figure 5, and the older stands beyond the *V. divaricata* advanced pioneer stage are presented by the stand described by Geldenhuys (1994), with no *V. divaricata* trees remaining but with a soil-stored seed bank of the pioneer species.

Musanga cecropioides in slash-and-burn sites in tropical moist forest

Most plots sampled in timber concession areas in southern Gabon covered mature forest, but some plots were sampled in old abandoned slash-and-burn sites along the transect lines (Geldenhuys et al. 2009, unpublished data). The total data set of over 600 plots on which trees with stem DBH ≥ 30 cm were sampled in four timber concession areas (Guietso, Moabi, Ndende and Mayumba) were searched for plots containing at least one Parasolier tree. Nineteen plots were extracted to assess what other forest species accumulated into the assumed initial pure Parasolier stands (see fig. 6B, C & D). The older stands beyond the Parasolier advanced pioneer stage are presented by the stands described by Geldenhuys et al. (2009), with no Parasolier trees remaining. The sixteen Mayumba plots each covered 0.2 ha (c. 25 m radius circular plots), and the other plots each covered 0.126 ha (20 m radius circular plots).

Ravenala madagascariensis in Manombo Special Reserve, south-eastern Madagascar

No sampling was done of the associated tree species in the stands dominated by or having plants of *R. madagascariensis*. General observations in different parts of the Manombo Special Reserve were considered adequate for the rapid assessment for a draft management plan done in 1994 (Anonymous 1996). The observed patterns of colonizing forest species into the almost pure stands of *R. madagascariensis* were similar to observations in many other areas, such as *Strelitzia nicolai* stands in KwaZulu-Natal Coastal Dune forest in South Africa.

RESULTS

Virgilia divaricata on Southern Cape Afrotemperate forest margins

In total twenty species, other than *V. divaricata*, with tree DBH ≥ 5 cm were present on the six plots (table 1). Five to nine other forest species per 0.04 ha plot became established within each of the initial *V. divaricata* pioneer stands. The mean DBH of the seven *V. divaricata* trees on these plots was 17.4 cm, and of the 276 trees of the accumulating forest species was 18.7 cm. Fifteen of the forest species are

Table 2 – Density and basal area of species of trees with DBH ≥ 30 cm accumulating in developing pioneer stands of Parasolier (*Musanga cecropioides*), sampled on nineteen plots in tropical moist forest, southern Gabon.

*Commercial timber species

Species	Stems /ha	Basal Area m ² /ha
<i>Musanga cecropioides</i> R.Br.	15.9	3.50
<i>Xylopia aethiopica</i> (Dunal) A. Richard	6.4	1.27
<i>Berlinia bracteosa</i> Benth.*	2.0	0.56
Mwamba	2.0	0.22
<i>Ricinodendron heudelotii</i> (Baill.) Pierre ex Pax & Hoffm.	1.7	0.89
<i>Desbordesia glaucescens</i> (Engl). Tiegh.*	1.7	2.68
<i>Aucoumea klaineana</i> Pierre*	1.4	0.26
<i>Coula edulis</i> Baill.	1.4	0.31
<i>Milicia excelsa</i> C.C.Berg*	1.1	0.33
<i>Coelocaryon preussii</i> Warb.*	1.1	0.23
<i>Ctenolophon englerianus</i> Mildbr.	1.1	0.87
<i>Zanthoxylum heitzii</i> Aubrev. & Pellegr.*	1.1	0.32
<i>Dacryodes pubescens</i> (Vermoes.) H.J. Lam.	1.1	0.36
Faux Tiama	0.8	0.17
Moubouba	0.8	0.22
Mouamba	0.8	0.69
<i>Maesopsis eminii</i> Engler	0.8	0.21
Diborila	0.8	0.48
Mougnonzou	0.6	0.09
<i>Uapaca</i> species (Rickio)	0.6	0.09
<i>Scyphocephalum ochocoa</i> Warb.*	0.6	0.54
<i>Uapaca</i> species (<i>Uapaca</i>)	0.6	0.18
Mouboussi	0.6	0.35
<i>Entandophragma congoense</i> A.Chev.*	0.6	0.40
Vemo	0.6	0.22
Dironda	0.6	0.06
<i>Cola lizae</i>	0.6	0.21
<i>Dacryodes macrophylla</i> (Oliv.) H.J.Lam	0.6	0.49
Douvouga	0.6	0.12
*9 Commercial species	2.5	0.74
25 Non-commercial species	7.0	1.75
Mean values per stand	58.5	18.79

bird/mammal dispersed, and four have small or winged non-animal dispersed seeds. The one alien tree species (*Acacia melanoxylon*) has hard-scaled legume seed with an aril and is bird-dispersed. The initial pioneer stand (fig. 5) eventually facilitated regeneration of shade-tolerant forest species towards mixed-species regrowth forest (table 1) and eventually mature forest (Geldenhuys 1993, 1994) in a natural way, i.e. a typical succession process.

Musanga cecropioides in slash-and-burn sites in tropical moist forest

A total of 63 tree species were recorded on the nineteen plots and apart from Parasolier, included a mean of five other species (range 1 to 11 other species) per plot (mostly 0.2 ha in size). The stems represented seventeen commercial timber species of which eight had two or more stems per plot and nine had one stem per plot. Parasolier contributed 3.48 m²/ha but its contribution decreased with an increasing contribution of other species. In an abandoned slash-and-burn site in southern Cameroon two trees of Limba (*Terminalia superba* Engl. & Diels) developed over 50 years into stem diameters of 50 and 80 cm DBH with a clean cylindrical bole of 17 m (C.J. Geldenhuys, personal observation, 2006).

The disturbed forest (as in fig. 6B, C & D) developed through different recovery stages (table 2) to mature forest (Geldenhuys et al. 2009), each with its own biodiversity component, from the mono-specific stands into mixed species stands, although not all stages were represented here. Species with characteristics to establish and grow in the disturbed forest sites facilitated the development of species with different characteristics towards mature forest, in a natural, typical succession process in the tropical moist forests of the Congo Basin. Several of the recovering species are important commercial timber species (table 2) and several of these do not regenerate in the mature forest (Geldenhuys et al. 2009).

Ravenala madagascariensis in Manombo Special Reserve, south-eastern Madagascar

The general observations have shown that *R. madagascariensis* seems to have several functions in the recovery process towards natural forest (Anonymous 1996): it is relatively fire resistant thereby protects the edge of true forest species; it recovers rapidly on the site through sprouting after a fire; it can colonise areas with very poor soils; it serves as a perch for seed dispersers; and it functions as a nurse stand for the establishment of the regenerating other forest species to serve as focus points for the expansion of forest. Its role in the succession process and forest recovery should be explored further.

NATURAL FOREST RECOVERY VIA PLANTED AND NATURALIZED STANDS OF INTRODUCED TREE SPECIES: A SHORT OVERVIEW

Planted stands of introduced tree species, typically used in commercial forestry plantations, facilitate the establishment of natural forest species in the understorey of such stands (Parrotta 1995, Geldenhuys 1996b, 1997, Loumeto & Huttel



Figure 9 – Natural forest tree species regenerating in the understorey of planted stands of: A, *Pinus patula* in Entabeni plantation, Soutpansberg (from Geldenhuys 1997 study); B, *Acacia melanoxylon* in the Bloukrans State Forest, Southern Cape study (from Geldenhuys 1996b study), both in South Africa, and C, *Eucalyptus alba* × *urophylla* plantations in the Pointe Noire area, Democratic Republic of Congo (from Loumeto & Huttel 1997 study; personal observation).



Figure 10 – Rapid colonization of cleared areas after mining in the Tshikapa area, Democratic Republic of Congo, by A, *Chromolaena odorata* (front left of cleared area); followed by B & C, the natural regeneration of *Trema orientalis* and *Musanga cecropioides* (present but not obvious on photos) and eventual over-topping and out-shadowing *C. odorata*.

1997, Lugo 1997, Parrotta & Turnbull 1997, for global examples; Parrotta et al. 1997b, Geldenhuys & Delvaux 2007). Species of the overhead stand, development stage from young to old stands (influencing stand density and stand height), and distance away from the source of plant propagules are factors that determine the rate and species composition of recovery of natural forest species. All the main canopy tree species of the surrounding natural forest established within the planted stands of Australian Blackwood (*Acacia melanoxylon*) in the Southern Cape Afrotropical forests, South Africa (fig. 9; Geldenhuys 1996b). The South African part of a worldwide study on how planted tree stands facilitates the establishment of natural forest species (Parrotta & Turnbull 1997), was done in the Limpopo Province in several pine stands (*Pinus patula* Schiede Schltdl. & Cham. of different age and old *P. taeda* L. and *P. elliottii* Englem.), one *Eucalyptus saligna* Sm. stand and one *Acacia mearnsii* De Wild. stand (Geldenhuys 1997). The study recorded 170 natural forest species in 62 small plots (0.04 ha plot for trees; 0.008 ha plot for understorey vegetation), including 62 tree and 33 woody shrub and climber species of the surrounding natural forest, with 72% of the 95 woody species dispersed by animals. Species richness, stem density and size (height and stem diameter) of woody regeneration in the *P. patula* stands increased with increasing stand age. The differences in species composition, density and size of the woody regeneration were not significant between different mature overhead species but geology (representing nutrient and drainage) and

temperature (represented by altitude and radiation index) had stronger influences on the variation in understorey woody regeneration. Better regeneration underneath canopy gaps and spots of reduced crown density or near the plantation margin suggested that light intensity and quality in the understorey affect regeneration success of woody regeneration. When planted trees in a stand grow taller, tree height, crown density, crown volume and clear bole length become more variable and gaps of variable size and shape start to develop to enable more species to regenerate and become established.

The mining environmental management code (IFC Performance Standard 6, April 2006) does not allow the use of invasive alien plants in vegetation rehabilitation actions. In a mining rehabilitation project in the Democratic Republic of Congo, trifid weed (*Chromolaena odorata* (L.) King & H. Rob.) quickly established in cleared sites of slash-and-burn agriculture and mining (Geldenhuys 2008). The seed banks of trifid weed are everywhere, and germinate rapidly in exposed sites. The fast developing weed cover prevents erosion, adds litter to the site which initiates recovery of the nutrient cycling process. Natural forest pioneer tree species (*Trema orientalis*, *Musanga cecropioides*, *Macaranga* species and others) became established and grew through the trifid weed cover and eventually over-topped and out-shadowed it to start the forest recovery process (fig. 10); all with no site preparation and planting of costly nursery-grown plants.

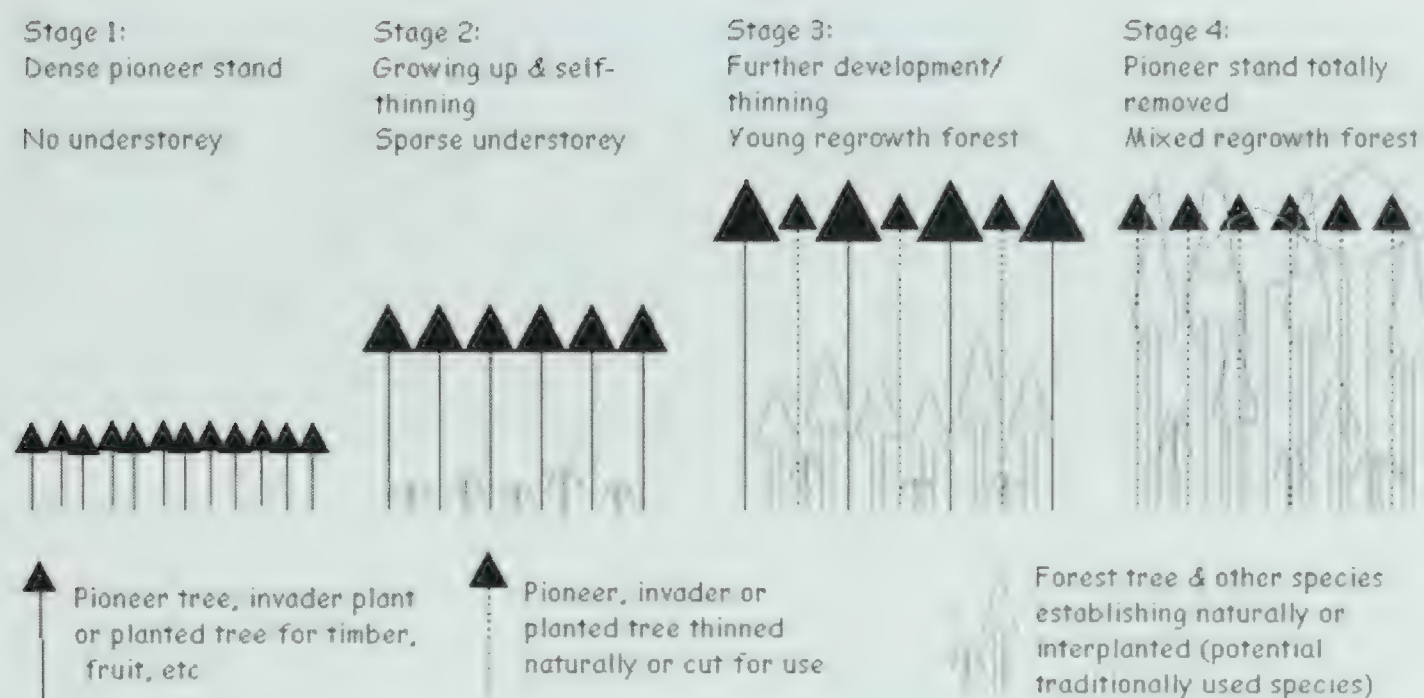


Figure 11 – Conceptual model of the relationship between stand development stage and the establishment of understorey vegetation from the natural forest (Geldenhuys 1999).

DISCUSSION

General concept and process

The indigenous pioneer tree species presented above, *Virgilia divaricata*, *Musanga cecropioides* and *Ravenala madagascariensis*, typically facilitate the recovery of disturbed sites, starting from mono-specific stands to species-diverse regrowth stands that become more similar to the surrounding mature forest in terms of species composition and stem sizes. This has been shown for other native pioneer tree species in South Africa such as *Acacia karroo* (with different current names) (Von Maltitz et al. 1996) and *Trema orientalis* (Scheepers 1978), but also for *Virgilia divaricata* (Phillips 1926, Van Daalen 1981, Geldenhuys 1994). The examples mentioned above show a recovery process similar to those observed and described for within stands of planted introduced timber species and naturalized perceived alien invader species in forests, such as the pines, eucalypts, acacias, and even triffid weed. The light-demanding alien species with invasive tendencies have one or more characteristics in common with the native pioneer species (Geldenhuys 1986, 1996b, Geldenhuys et al. 1986):

- they are also pioneer trees, shrubs and climbers in their natural environments;
- they have wind or animal-dispersed (birds, primates and bats) fruits or have long-living hard-coated seeds, and several develop long-living soil-stored seed banks;
- they rapidly colonize sites disturbed in terms of forest structure and cover;
- they are generally easy raised, and fast-growing in the open.
- they are intolerant of shade (cannot establish successfully under their own canopy or the closed forest canopy)
- they buffer the more variable and extreme conditions of regularly disturbed grassland, shrubland and agricultural fields and facilitate the establishment of shade-tolerant forest species
- many have several (3+) important uses.

However, they have a competitive advantage outside of their natural environment because they do not have their natural enemies which control them in their native environments.

The similarities in general function between native and introduced pioneer tree species provide a basis to develop a common concept for forest rehabilitation and recovery in the natural environment. Firstly, the natural disturbance processes in the landscape, mainly fire, confine natural forests to specific parts of the landscape (see Introduction and figs 2–4). Secondly, pioneer species (often represented by invasive alien species) establish in the disturbed landscapes after the disturbance has occurred, as part of the recovery process. With frequent disturbance in the landscape of the forest environment, the recovering vegetation remains in the pioneer state. Thirdly, the pioneer stands develop through a process of self-thinning which creates conditions for the establishment of species which are increasingly more shade-tolerant. They facilitate the development of the pioneer mono-specific stand towards a mixed-species regrowth natural forest. This general recovery process through pioneer stands (both native and alien) is shown in figure 11.

Rehabilitate forest outside of the fire zone

Not all areas that appear to be suitable for forest rehabilitation could be successfully converted to forest. Areas within the fire pathway (figs 2 & 3) should be avoided unless costly fire protection actions could be implemented. However, even with such actions the severe uncontrollable fires during irregular extreme conditions could destroy all rehabilitation efforts (fig. 4). Rehabilitation actions should focus on areas near the forest margin which are clearly inside the 'fire-shadow' areas such as known cleared forest sites and within river/stream bank vegetation zones. For example, figure 12 shows the planting of various, mainly pioneer, tree species around the special forest reserve for the protection of the rare tree Sohisika (*Schizolaena tampoketsana* Lowry, G.E.Schatz, J.-F. Leroy & A.-E. Wolf) in the highlands north of Antananari-



Figure 12 – The special forest reserve (A) in the highlands north of Antananarivo, Madagascar, established for protecting the rare tree Sohisika (*Schizolaena tampoketsana*). The coppicing bushy plants of Sohisika in the grassland immediately above the western boundary (B & C) show the role of regular fires in the area which also show that the plantings in the grassland above the forest (left) were done within the fire zone, with a risk of being destroyed by fire.

vo, Madagascar (personal observation, April 2010). However, the plantings were done within the fire zone and extreme fire events could destroy all planting effort and costs.

Manipulative conversion of pioneer and alien tree stands towards natural forest recovery

In grassland and shrubland systems, most invasive alien species compete directly with the grassland/shrubland systems and species and need to be cleared or removed to restore the natural systems. In general most invasive alien plant species in the natural forest environment are intolerant of shade whereas most natural forest species are shade-tolerant. In this environment most invasive alien species facilitate (nurse) the recovery of the natural forest system and species (biodiversity). Clearing light-demanding invasive alien species in the natural forest environment followed by planting natural forest species is therefore unnecessary. Stand manipulation through selective thinning can be implemented to facilitate the typical succession process, to convert alien plant stands towards regrowth native forest, and to provide in needs for firewood, poles and timber. This process has benefits over the conventional invasive alien clearing practice:

- it is a typical forest succession process which can be managed to achieve specific complementary objectives of forest protection, biodiversity recovery and provision in rural resource use needs;
- it is less expensive both in terms of clearing actions and establishing native tree species;
- it can provide useful substitute products to local resource users (firewood, poles, timber) during the conversion actions towards forest recovery;
- the pioneer stands can be a source of seedlings of medicinal and food plants for planting in rural home gardens or rehabilitation actions without a costly nursery .

Basic guidelines for practical conversion management of alien tree stands to regrowth forest

Four basic steps are required to rehabilitate natural forest from pioneer/invasive alien tree stands:

Step 1: zoning by main units in vegetation mosaics – Zone each potential rehabilitation area with natural vegetation and

different land uses by the end-points in alien plant removal, such as productive farmland or timber production areas, healthy riparian zones/stream bank, etc. This would include areas that need abrupt, total clearing of alien vegetation (shrubland, grassland, woodland); and areas that need gradual removal of alien stands ('forest', riparian zones, stream banks). Consider the potential user needs for the forest rehabilitation areas in terms of 'useful' pioneer or invasive species for small business development options (firewood, poles, timber, etc).

Step 2: zoning forest areas by forest stand development stages – Zone the pioneer /invasive alien plant stands within the forest environment (including stream areas) by the four main stand development stages (overhead composition and density; understorey woody vegetation size and density; fig. 12):

- **Stage 1:** Dense, young nurse stands; none to very few natural forest tree species in understorey; wait for nurse stand to undergo self-thinning.
- **Stage 2:** Dense but taller nurse stands; forest tree seedlings and saplings in small groups; selectively remove nurse stand stems to facilitate development and growth of forest tree seedlings into saplings and poles.
- **Stage 3:** Natural nurse stand thinning is in progress; forest tree clusters taller and expand laterally; selectively remove nurse stand stems within clusters of forest species to facilitate height growth and horizontal expansion of clusters.
- **Stage 4:** Scattered nurse stand trees; advanced stage of forest recovery; remove all remaining nurse stand trees in gaps and forest edge; use as a norm for the recovery of stages 1 to 3.

Step 3: implement stand manipulation in stand development stages 2 and 3 – The intensity of rehabilitation activities will vary according to the development stage (canopy and understorey) of each nurse stand. Carefully and gradually remove selected unwanted trees of the nurse stand of pioneer/planted/invasive alien species to enable regeneration of natural forest species to become established, naturally. Cut the selected stems for direct use or ring-bark them to die standing in the selective thinning (not clearing). Consider four golden rules:

1. Focus on the establishing forest species clusters;
2. Maintain a relatively closed nurse stand canopy to prevent regeneration and regrowth of the nurse stand species, but open it above forest species clusters to help the forest seedlings, saplings and poles to grow stronger, and to flower and fruit earlier to enable fruit/seed dispersers to help with the process;
3. Remove small suppressed or stunted sub-canopy stems of the nurse stand species to provide more growing space for the regeneration and growth of forest species in the understorey;
4. Keep the ground cover (herbaceous plants, litter, dead branches, etc) intact to prevent invader or pioneer species to become established.

Step 4: plant forest seedlings in spots without seedlings – Limit planting to spots in the stand with no forest seedlings or to specific species that do not disperse easily. Seedlings could be collected from clusters of seedlings (maximum 50% of the seedlings in dense clusters) from the nurse stand or the nearby natural forest. Do the planting during misty or rainy weather to ensure success.

The results from the various studies have shown that a pioneer or planted or naturalized nurse stand can be converted to natural forest, where this is not in the normal fire zone. It can be done much cheaper because nature does a large part of the job for free (birds and mammals carry many of the seeds into the stand). The manipulative ‘interference’ through selective thinning is simply to speed up the stand development process! A practice of repeated clearing of invader plants, for example in the riparian zone, can be changed into a system of regrowing forest with much reduced maintenance costs. The removed stems could be used for laths, poles, firewood, timber, depending on the development stage of the nurse stand. Medicinal plant crops and other forest species could be harvested from such stands. It is a different system, a different mindset and a different approach, with many hidden values to the owner of the land, adjacent communities in many areas, and society as a whole.

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- Manuscript received 23 Sep. 2010; accepted in revised version 11 Jan. 2011.
- Communicating Editor: Bonaventure Sonké.



***In vitro* propagation and *ex situ* conservation of *Drimia cryptopoda* and *Ledebouria nossibeensis*, two endangered endemic Hyacinthaceae from Madagascar**

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Background and aims – Several species of Hyacinthaceae are rare and critically endangered elements of the flora of Madagascar. To assist *ex situ* conservation measures in Madagascar we sought a simple, inexpensive yet efficient method of propagating such species, comparing the results with those from a standard method using two endangered species from two subfamilies.

Material and Methods – *Drimia cryptopoda* (Baker) Pfosser, Wetschnig & Speta (Urgineoideae) and *Ledebouria nossibeensis* (H.Perrier) J.C.Manning & Goldblatt (Hyacinthoideae), two of the most endangered Hyacinthaceae of Madagascar, were chosen to develop a protocol for *in vitro* propagation using a laminar flow cabinet, autoclave and prefabricated media on the one hand, and more readily available and low-cost items on the other.

Key results – Using the standard method, the induction of callus and regeneration of plantlets large enough to be transferred to pot culture was achieved in 8–12 weeks; the low-cost method also yielded plantlets, although in somewhat lower numbers.

Key words – *In vitro* propagation, *ex situ* conservation, Flora of Madagascar, Hyacinthaceae.

INTRODUCTION

Hyacinthaceae in Madagascar were revised by Perrier de la Bâthie (1938) in his treatment of Liliaceae in the Flora of Madagascar, which recognized six genera and fifteen species that are now considered to belong to Hyacinthaceae: *Dipcadi* Medicus (three species), *Hyacinthus* L. (one species), *Ornithogalum* L. (one species), *Rhodocodon* Baker (eight species), *Scilla* L. (one species) and *Urginea* Steinheil (one species). According to the classification of Hyacinthaceae proposed by Speta (1998a, 1998b) members of all the three old-world subfamilies occur in Madagascar: Urgineoideae Speta (*Rhodocodon*, *Urginea*), Ornithogaloideae Speta (*Dipcadi*, *Ornithogalum*) and Hyacinthoideae Link (*Hyacinthus*, *Scilla*).

Speta, in his treatment of Hyacinthaceae (Speta 1998a) and a revision of the genus *Scilla* s. lat. (Speta 1998b), made some substantial changes to Madagascan Hyacinthaceae. Within subfamily Hyacinthoideae, *Scilla nossibeensis* H.Perrier was transferred to *Resnova* (*R. nossibeensis* (H.Perrier) Speta). In their generic synopsis of sub-Saharan Hyacinthaceae Manning et al. (2004) presented a concept of very broad generic circumscriptions giving rise to further

changes in the nomenclature of Madagascan Hyacinthaceae, transferring *Scilla nossibeensis* and *Hyacinthus cryptopodus* Baker to *Ledebouria* (*L. nossibeensis* (H.Perrier) J.C.Manning & Goldblatt and *L. cryptopoda* (Baker) J.C.Manning & Goldblatt, respectively) on morphological reasons. Pfosser et al. (2006) showed that *Ledebouria cryptopoda* (Baker) J.C.Manning & Goldblatt is in fact a member of subfamily Urgineoideae and proposed the new combination *Drimia cryptopoda* (Baker) Pfosser, Wetschnig & Speta (fig. 1A). Wetschnig et al. (2007), using chloroplast DNA sequence data, found *L. nossibeensis* (fig. 1B) to be closely related to *L. hyacinthina* Roth., the type species of the genus.

While working over the last decade with colleagues at the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar (PBZT) it soon became apparent that several endemic species of Hyacinthaceae are rare and critically endangered in Madagascar, viz. *Drimia cryptopoda* (Pfosser et al. 2006) and *Ledebouria nossibeensis*. As early as 1938 Perrier de la Bâthie (1938) stated that *D. cryptopoda* (fig. 1A) was rare and in danger of extinction (“... rare, en voie de disparition et paraissant spéciale aux trachytes de l’Ankaratra”). More recently, the rediscovery of *L. nossibeensis* was re-

ported on the islands of Nosy Be and Nosy Faly (Anonymus 2006), where it was said to be threatened because of small population size and the construction of a hotel at one of the locations.

Several papers have appeared recently dealing with the *in vitro* propagation of Hyacinthaceae from South Africa (e.g. Fennel & Van Staden 2004) and India (e.g. Nair 1989). Biotechnology is a well established tool in plant conservation (Fay 1994), and several studies have discussed the use of *in vitro* propagation to reduce the pressure from collecting Hyacinthaceae for ethnobotanical uses (e.g. McCartan & Van Staden 1999, Afolayan & Adebola 2004). In Hyacinthaceae *in vitro* propagation is an established method for *ex situ* conservation as well as for horticulture.

In this paper we present results using a standard methodology as well as an easy, inexpensive and efficient method of *in vitro* culture for *Drimia cryptopoda* and *Ledebouria nossibeensis* in an effort to contribute to the *ex situ* conservation of these endangered species.

MATERIAL AND METHODS

This analysis is based on material from the *locus classicus* of *Drimia cryptopoda* (near the village Ambatondradama) and on material of *Ledebouria nossibeensis* from Nosy Bé (coordinates are withheld here because of the critically endangered status of these species). Vouchers of the cultivated specimens from which explants were taken are deposited at GZU (Herbarium of the Institute for Plant Sciences of Karl-Franzens-Universität Graz).

For the standard method, leaves were sterilized without prior cleaning in a sodium hypochlorite solution (DanKlorix™: 2.8% sodium hypochlorite) for 25–30 minutes, then wrapped in Mikrozyd Liquid™ (25% ethanol, 35% 1-propanol) soaked paper towels and put into a laminar flow cabinet for half an hour.

Transfer of explants was performed in a laminar flow cabinet: the sterilized leaves were cut in 1 × 1.5 cm pieces (explants), which were transferred (without rinsing with distilled water) onto the medium in culture vessels (P-5682 Sigma Phytacon™ Vessel, 76 mm high) with the abaxial side downwards. The first (proliferation) medium was Phytamax™ Orchid Multiplication Medium P6793 (data sheet available at: <http://www.sigmaaldrich.com>), which contains N⁶-benzylaminopurin (BA) (2.0 mg/l) and α -Naphthalene acetic acid (NAA) (0.5 mg/l). A control of the pH can be omitted because MES (4-morpholinoethansulfonic acid) as a biological buffer keeps the pH at 5.5 after autoclaving the media at 125°C and 1.4 bar for 20 minutes. To enhance differentiation after the proliferation stage, the callus was transferred to a new, hormone free medium (Phytamax™ Orchid Maintenance Medium P-6668; data sheet: <http://www.sigmaaldrich.com>). Illumination of the culture vessels was provided by light bulbs (Philips Fluotone TL-D 35W/33 standard) using a 12 hour dark/light rhythm.

The temperature was kept at 18°C during the dark phase and at 25°C during the light phase. Sterilization of culture vessels with media and working tools was performed in an autoclave (125°C and 1.4 bar for 20 minutes).

The alternative, low-cost method differs from the standard method in several ways. For the sterilization procedure, Mikrozyd Liquid™ was substituted by ethanol (70%). The transfer of explants was performed over steam, and only one medium was used. The alternative medium consisted of sucrose (20 g/L), agar (for cooking, 6–8g/L) and fertilizer (e.g. Hyponex™ 3g/L). Culture vessels were exposed to daylight (no direct sun) using a 12 hour dark/light rhythm. During the propagation phase the temperature varied from 17 to 24°C. Sterilization of culture vessels with media and working tools was performed in a pressure cooker for 30 minutes. All of the ingredients are readily available in Madagascar.

RESULTS AND DISCUSSION

Standard method

Just five days after the start of *in vitro* culture of *Ledebouria nossibeensis* callus formation could be observed (fig. 1C) and three weeks later proliferating callus had developed along with leaves up to 5 cm long (fig. 1D). Differentiation into roots, leaves and bulbs was considerably more rapid on hormone free medium. Callus transferred onto the hormone free medium showed good differentiation after 1–2 weeks (fig. 1E). After 6–8 weeks plants up to 10 cm long had developed, with good root formation, clearly visible bulbs and stalked leaves. Depending on the size of the transferred callus, 50–100 or more plantlets were obtained (as callus proliferation did not stop completely on the hormone free medium). The plantlets of *L. nossibeensis* showed red spotted leaves (fig. 1F).

Drimia cryptopoda showed a delayed and reduced formation of callus and differentiation into plantlets, although about fifteen plants per explant were obtained.

Alternative, low cost method

Fourteen days after *in vitro* culture initiation *L. nossibeensis* showed callus initiation and differentiation into plantlets with both roots and leaves. No significant callus was observed. The yield per explant was 5–15 plantlets.

Multiplication of *Drimia cryptopoda* with this method was not possible. After *in vitro* propagation plantlets were transferred onto a non sterile sand-loam mixture. No loss of plants was observed after transfer.

General discussion

The standard method allows for the production of an almost unlimited number of plantlets of both species in a short time. The alternative method offers a useful procedure that is suitable for the conditions in Madagascar because of the the low-cost technical and chemical equipment needed is readily available. A disadvantage of this method is a considerably reduced callus initiation and proliferation. However, this can be compensated by using an increased number of explants, which is not a problem because of the number and size of the leaves of *L. nossibeensis*. Another disadvantage is the recalcitrance of *D. cryptopoda* in responding to this method. Contamination is not a significant challenge because of the

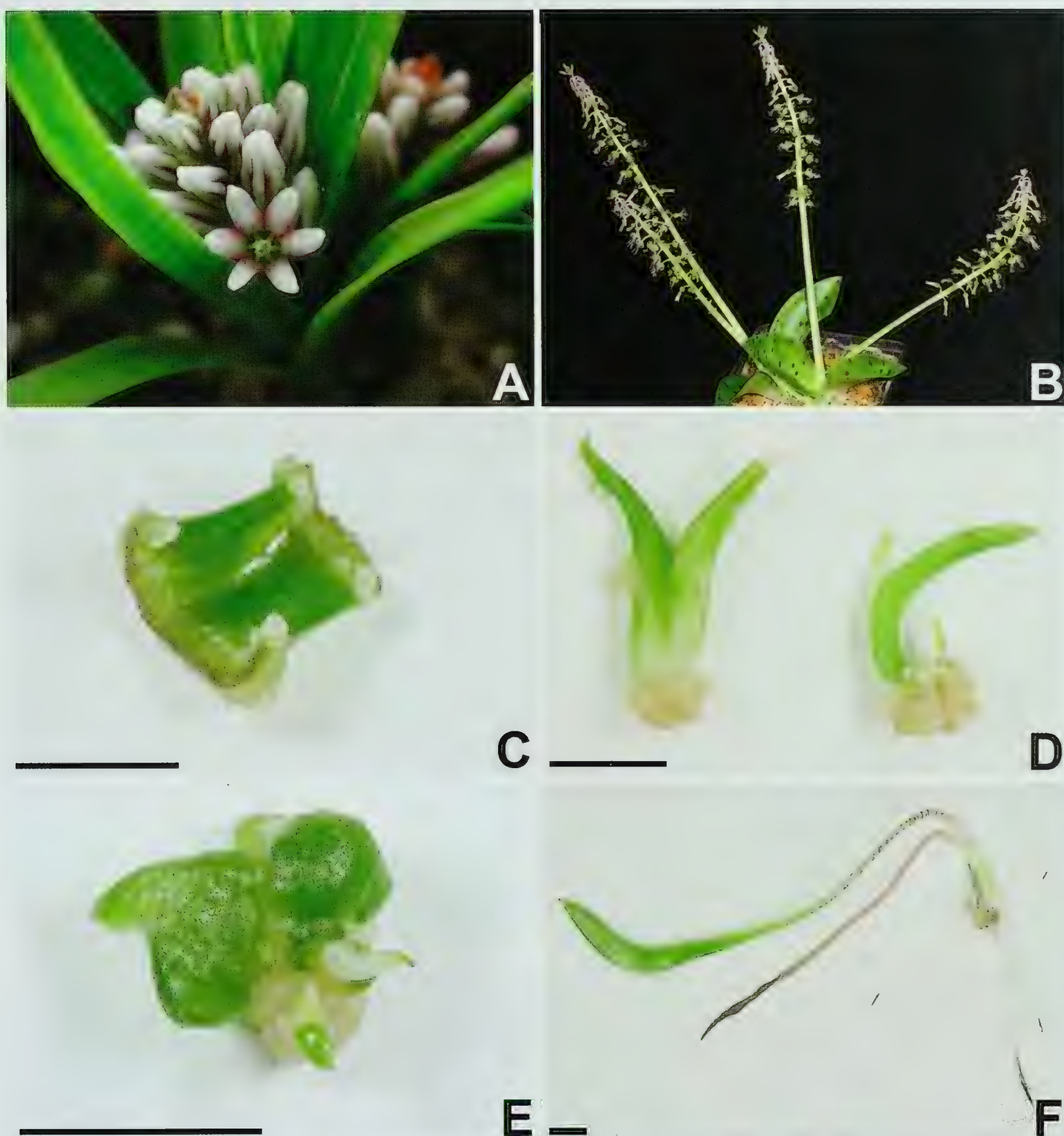


Figure 1 A, *Drimia cryptopoda*: 3.5 year old plant in flower; B–F, *Ledebouria nossibeensis*: B, 3.5 year old plant in flower; C, callus proliferation on leaf explants after five days on culture medium P6793; D, leaves arising from callus with secondary callus and stem proliferation after three weeks on culture medium P6793; E, root and leaf primordia after two weeks on culture medium P6668; F, regenerated plant with bulb, roots and leaves after twelve weeks (four weeks on culture medium P6793, eight weeks on P6668); scale bars: 1 cm.

short time required for *in vitro* culture. During our study no loss caused by contamination was observed.

ACKNOWLEDGMENTS

We would like to thank the Muséum National d'Histoire Naturelle (P) and the Sukkulenten-Sammlung Zürich (ZSS) for the loan of valuable herbarium material.

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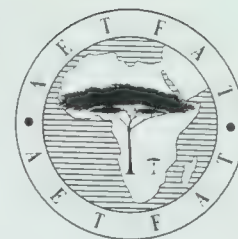
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- Manuscript received 30 Sep. 2010; accepted in revised version 25 Oct. 2011.
- Communicating Editor: Porter P. Lowry II.



Conservation d'*Angraecum longicalcar*, une orchidée menacée et endémique de Madagascar

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Conservation of *Angraecum longicalcar*, a threatened and endemic orchid of Madagascar

Background – The Royal Botanic Gardens Kew has developed a conservation program for *Angraecum longicalcar* (Bossé) Senghas, a threatened orchid species in the Ambatofinandrahana region of Madagascar. This species is listed as ‘Critically Endangered’ by the IUCN Red List of Threatened Species. It is facing a disturbance and a progressive decrease of habitat due to bush fires. Only 141 shoots persist in the wild.

Methods – *In vitro* seed germination, reintroduction of seedlings and *in situ* conservation of the seedlings in collaboration with the local community.

Key results – This species is endemic to Madagascar and occurs in two localities on four rocky marble outcrops at Mahavanona-Ambatofinandrahana. Flowers were hand pollinated to assist fruit production. Eight hundred and seventy-six seedlings were produced by seed germination and grown in the greenhouse at Parc Tsimbazaza at Antananarivo (Madagascar). Fifty seedlings were foremost transported and then acclimatized in a shadehouse to the site before planting in the wild.

Key words – Orchidaceae, *Angraecum longicalcar*, extinction, conservation, *ex situ*, *in situ*, micropropagation, hand pollination, reintroduction.

Contexte – Le Jardin botanique royal de Kew a développé un projet de conservation d'*Angraecum longicalcar* (Bossé) Senghas, une espèce d'orchidée menacée et présente dans la région d'Ambatofinandrahana à Madagascar. Cette espèce est en danger critique d'extinction selon la liste rouge de l'UICN. Elle est confrontée à une diminution progressive de son habitat résultant des feux de brousse. Seulement 141 pieds persistent à l'état sauvage.

Méthodes – Germination *in vitro* de graines, réintroduction de plantules obtenues et conservation *in situ* des plantules en collaboration avec la communauté locale.

Résultats-clés – Cette plante est endémique de Madagascar et a été rencontrée dans deux localités restreintes sur quatre affleurements rocheux formés de cipolins à Mahavanona-Ambatofinandrahana. Huit cent soixante-seize plantules ont été obtenues par la méthode de germination *in vitro* de graines de quelques fruits obtenus par pollinisation manuelle. Elles sont stockées dans une serre au Parc de Tsimbazaza à Antananarivo (Madagascar). Cinquante individus ont été par la suite transportés et acclimatés sous ombrière à Ambatofinandrahana avant de les transplanter ultérieurement *in situ*.

INTRODUCTION

Madagascar possède une grande richesse en orchidées; parmi les mille espèces répertoriées actuellement, environ 90% sont endémiques (Cribb et al. 2005). Malheureusement, les orchidées sont de plus en plus menacées d'extinction en raison de la destruction progressive de leur habitat et de la collecte abusive au sein de leurs populations naturelles. Des observations dans la région du Sud-Est de Madagascar ont

montré que seuls quelques individus de *Grammangis spectabilis* Bossé & Morat persistent dans une seule localité, de même que *Erasanthe henrici* (Schltr.) P.J.Cribb, Hermans & D.L.Roberts et *Angraecum longicalcar* (Bossé) Senghas sur les Hauts plateaux (Cribb & Hermans 2009). Cependant, les recherches sur les orchidées de Madagascar demeurent incomplètes. Par exemple, peu de recherches sur l'écologie des espèces ont été faites. De nombreuses espèces sont connues

uniquement par des échantillons collectés depuis plusieurs décennies. Certains échantillons portent de plus des informations insuffisantes et incomplètes, et sont souvent indisponibles pour les chercheurs et les communautés locales.

Face à ces enjeux, le Jardin botanique royal de Kew (RBG Kew) s'est investi depuis une quinzaine d'années dans les recherches sur les orchidées de Madagascar. Ces recherches ont permis de découvrir de nouvelles espèces comme *Eulophia epiphytica* épiphyte au Sud-est (Cribb et al. 2002), et le nouveau genre *Erasanthe* dans la région d'Isalo (Cribb et al. 2007), mais aussi de produire des ouvrages tels que *Orchids of Madagascar* (Hermans et al. 2007) et le *Field guide to the Orchids of Madagascar* (Cribb & Hermans 2009). Une traduction en version malgache du *Field guide* est de plus envisagée pour surtout satisfaire la population locale.

Depuis 2003, le RBG Kew a développé un projet de conservation qui cible certaines espèces d'orchidées rares et en danger de Madagascar, et ce, en collaboration avec le Centre Technique et Horticole d'Antananarivo (CTHA) et le Parc Botanique et Zoologique de Tsimbazaza (PBZT). Ce projet vise à évaluer le statut de conservation des orchidées en danger de Madagascar, enrichir les banques de graines en particulier pour les espèces en danger dans un but de futur de réintroduction, intégrer et encourager la communauté locale à participer dans les activités de conservation, et élaborer un plan d'aménagement pour certaines zones renfermant des orchidées menacées.

Angraecum longicalcar est une orchidée endémique de Madagascar. Elle n'a été signalée que dans trois régions de l'île (fig. 1). Elle a été découverte aux alentours du lac Itasy en 1965 sur des rocaillies de trachyte (Du Puy et al. 1999). Elle a par la suite été également collectée dans une localité à Bongolava en 1990 dans une galerie forestière à *Pandanus*, *Tambourissa*, *Adina* et *Harunga*. En outre, elle a été trouvée à Mahavanona-Ambatofinandrahana sur quatre affleurements rocheux à cipolins (appendice électronique 1). Cette localité abrite son unique sous-population connue actuellement. Cette sous-population présente au total 141 individus formant sept petits groupes appelés "colonies". Cette espèce n'est pas fortement collectée par la population locale. Elle récolte quelques feuilles pour faire des infusions contre certaines maladies gastriques et génitales légères (Rajaovelona L., comm. pers.). Par contre, son milieu d'origine fait l'objet régulièrement de feu de brousse.

Elle est donc considérée comme une espèce en danger critique d'extinction selon l'UICN (IUCN 2011) en raison de sa distribution restreinte sur les hauts plateaux du centre et de la destruction progressive de son habitat. Ces raisons nous ont poussées à la choisir comme espèce cible pour le projet pilote des projets de conservation des orchidées menacées de Madagascar.

MATÉRIEL ET MÉTHODES

Il est important que les acteurs de la conservation connaissent la stratégie de la reproduction des espèces ciblées pour pouvoir estimer l'espérance de vie de ces dernières (Roberts 2003). Pour vérifier cette hypothèse, des études de terrain ont été effectuées en 2004 afin de récolter des données

sur l'écologie de la reproduction (pollinisation, mode de reproduction) et la phénologie (stade floral et fructification, germination des graines) d'*Angraecum longicalcar* (Rajaovelona 2005). La phénologie des fleurs depuis le stade de bouton floral, le pic de floraison jusqu'au stade de fanaison a été observée. Au moment de la floraison, des pollinisations manuelles (autofécondation et fécondation croisée) ont été réalisées sur certaines fleurs de quelques pieds de la plante (appendice électronique 2). Trois mois et six mois après les pollinisations manuelles, des fruits ont été récoltés pour réaliser une multiplication *in vitro* des graines. Cette multiplication a été effectuée au sein du laboratoire du Centre Technique et Horticole d'Antananarivo (CTHA) en utilisant le milieu de culture MS (Murashige & Skoog 1962). Ce dernier est utilisé pour produire des plantules ou vitro-plants à transférer pour la suite vers le milieu d'origine afin de renforcer la population naturelle restante d'*A. longicalcar*.

A présent, RBG Kew entame la phase de conservation *in situ* visant premièrement à protéger l'habitat naturel la population sauvage restante de la plante et deuxièmement à réintroduire les vitro-plants vers le site d'origine. De ce fait, RBG Kew ont intégré la communauté de base ou COBA, une association qui groupe la population locale et l'école primaire publique à Mahavanona-Ambatofinandrahana à participer dans cette phase. Au début, des séances de sensibilisation et de formation sur *Angraecum longicalcar* concernant le maintien de la population sauvage et des soins nécessaires

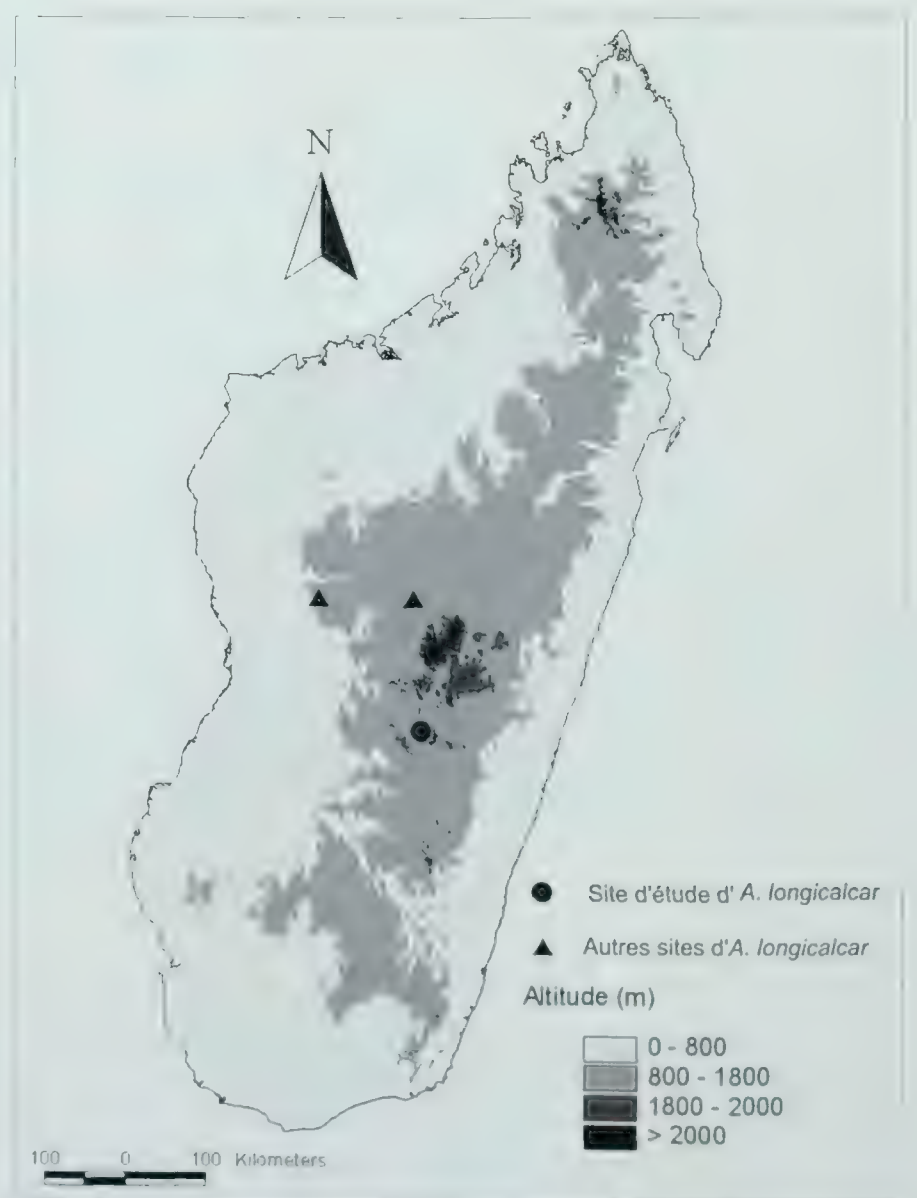


Figure 1 – Distribution d'*Angraecum longicalcar*. Définition des étages altitudinaux d'après Humbert & Cours Darné (1965).

à apporter aux vitro-plants obtenus ont été effectuées. La sauvegarde de la population sauvage d'*A. longicalcar* a été réalisée par le COBA, l'acclimatation des vitro-plants faite par l'école primaire et leur réintroduction sera par la suite effectuée en collaboration avec le COBA.

RÉSULTATS

Seaton (2010) suggère que la forte production de graines par la méthode *in vitro* est indispensable car la probabilité des plantes d'orchidées de vivre dans un environnement contenant le mycorhize adéquat pour la germination des graines et le développement de la plante est très faible. D'après nos observations de terrain réalisées en 2004, aucun fruit n'a été produit naturellement. Ceci suggère que les pollinisateurs nocturnes spécifiques, qui pourraient être des Sphingidés possédant une longue trompe proportionnelle à la présence d'un long éperon chez *Angraecum longicalcar*, sont absents dans le site de Mahavanona. Les jeunes individus rencontrés sont des rejets provenant de la multiplication végétative se trouvant à la base des plantes âgées (Rajaovelona L., obs. pers.). La pollinisation manuelle s'avère donc indispensable afin de produire de fruits et de mettre en œuvre une stratégie de conservation *ex situ* de la plante.

Le fruit collecté trois mois après la pollinisation manuelle est encore très vert et de petite taille par rapport à celui récolté trois mois plus tard. Le taux de germination *in vitro* des graines est de 20%. Six mois après la pollinisation, la capsule est bien développée, verte jaunâtre mais encore fermée contenant des graines encore immatures (certaines blanchâtres et d'autres brunâtres). Cependant, le taux de germination est d'environ 90%. La multiplication *in vitro* a donné naissance à 876 vitro-plants. Ces derniers ont été plantés dans des pots plastiques quand ils ont atteint 10 cm de taille. Dans le cadre de la réalisation de ce projet en collaboration avec le PBZT, RBG Kew a construit une serre vitrée pour orchidées au sein du PBZT; les plantules d'*Angraecum longicalcar* y sont installées et acclimatées (appendice électronique 3). D'autres espèces d'orchidées comme *Angraecum magdalenae*, *Bulbophyllum hamelinii*, *Paralophia epiphytica* multipliées par micropropagation y sont également cultivées.

En 2007, des démonstrations sur le terrain munies de distribution de brochures montrant les méthodes de pollinisation manuelle, de protection du site naturel ainsi que les entretiens nécessaires pour les vitro-plants à réintroduire ont été effectuées. Actuellement, la COBA assure la protection des sites sauvages d'*A. longicalcar* en y installant autour annuellement des pare-feux. A chaque période de floraison, les membres de la COBA assurent la pollinisation manuelle d'une à trois fleurs de la plante pour fournir des fruits aux banques de graines (Millenium Seed Bank) et pour vérifier l'existence ou non de graines germées dans le milieu naturel.

En 2010, 25 vitro-plants plus petites (20 cm) et 25 autres pieds plus grands (40 cm) ont été transportés à Mahavanona-Ambatofinandrahana. Une ombrière en bambou (appendice électronique 4) y a été construite pour les acclimater et les adapter pendant quelques mois au climat de la région. La COBA et l'école primaire s'occupent de l'entretien de ces plantules (rempotage, arrosage, désherbage et nettoyage des

feuilles). Des fiches de suivi ont été élaborées par RBG Kew et sont remplies mensuellement par les instituteurs et les membres de la COBA qui assurent l'entretien et le suivi de l'état des plantules.

DISCUSSION ET CONCLUSION

L'efficacité de ce projet dépend étroitement de l'enthousiasme de la population locale dans l'accomplissement des différentes tâches qui lui ont été confiées.

Il est à noter que la région d'Ambatofinandrahana est une zone riche en orchidées. Sa protection s'avère donc importante vu que les sites où vivent ces plantes sont facilement accessibles et sont dévastés régulièrement par les pratiques de feux de brousse. Cette flore particulière mériterait d'être visitée et pourrait favoriser la venue de touristes ce qui signifie un apport financier pour la communauté locale dans cette région. La conservation d'*Angraecum longicalcar* est donc une initiation à la conscientisation de la communauté locale à la valeur de la flore malgache en particulier des orchidées. Cette sensibilisation se fait progressivement afin d'atteindre l'objectif de conserver durablement les espèces d'orchidées en danger de Madagascar. Pour aider la communauté locale à contribuer au projet, du matériel comme les charrues pour mettre les pare-feux, les arrosoirs et les pots plastiques pour les rempotages des vitro-plants, leur ont été fournis. Aussi, nous avons fait don de livres et d'ouvrages sur l'environnement et sa conservation pour l'école primaire publique.

La réintroduction des cinquante vitro-plants sera effectué sur un autre site formé d'affleurement rocheux se trouvant dans la même localité et représentant les mêmes aspects physiques d'exposition au soleil, de substrat cipolins et de végétation xérophytique.

Une analyse d'ADN de la population sauvage d'*Angraecum longicalcar* ainsi que des vitro-plants sera réalisée pour vérifier s'il pourrait exister une variation génétique des pieds de la plante sur le site d'origine et le site de réintroduction. Ce programme de réintroduction d'*A. longicalcar* pourrait servir de modèle pour d'autres projets de conservation dans un futur proche, en l'occurrence sur des actions de conservation des orchidées en danger critique d'extinction à Madagascar.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible au format pdf sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> > SBB50 > dossier 527) et comprend: (1) colonie d'*Angraecum longicalcar* sur collines rocheuses à cipolins à Analabebiby- Mahavanona; (2) pollinisation manuelle *in situ* de fleurs d'*Angraecum longicalcar*; (3) serre à orchidées dans le Parc Botanique et Zoologique de Tsimbazaza; (4) cinquante plantules d'*Angraecum longicalcar* ont été acclimatées avant leur réintroduction *in situ* sous une ombrière au village de Mahavanona-Ambatofinandrahana.

REMERCIEMENTS

Nos vifs remerciements s'adressent aux organisateurs de l'AETFAT 2010 et aux éditeurs de la revue *Plant Ecology and Evolution* pour avoir préparé les Proceedings de l'AETFAT 2010. Un grand merci au Dr David Roberts pour avoir partagé ses connaissances et ses expériences sur l'écologie et la conservation des orchidées en particulier de cette espèce. Ce projet a bénéficié d'un financement de la part des Friends of Kew. Notre reconnaissance s'adresse aux membres du Vondron'Olonia Ifotony et à l'Ecole Publique Primaire de Mahavanona-Ambatofinandrahana pour leur motivation à conserver l'espèce *Angraecum longicalcar*. Toute notre gratitude va aussi au Dr Mijoro Rakotoarinivo, au Dr Hélène Ralimanana, aux deux relecteurs et à l'Editeur, le Dr Tariq Stévant, pour leurs commentaires constructifs dans la rédaction de ce manuscrit.

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Manuscript received 23 Sep. 2010; accepted in revised version 19 Dec. 2011.

Communicating Editor: Tariq Stévant.



Evaluation du risque d'extinction des *Cedrelopsis* (Rutaceae) de Madagascar

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Assessing the extinction risk for *Cedrelopsis* (Rutaceae) in Madagascar

Background and methods – *Cedrelopsis* (Rutaceae), commonly known as Katrafay, is an endemic genus of Madagascar and consists of eight species of trees and shrubs growing on different substrates and in primary and/or modified ecosystems. These species of *Cedrelopsis* are plant parts most used plants for several purposes. Thus, an ecological assessment was undertaken in aim to understand the pressures and threats to populations, define their conservation status, and establish a strategy for sustainable management.

Key results – Approximately 65 to 100% of subpopulations of *Cedrelopsis* are in sites with no appropriate conservation measure. Timber and habitat loss are the major threats. *Cedrelopsis procera* is critically endangered, while *C. gracilis*, *C. longibracteata*, *C. ambanjensis*, and *C. rakotozafyi* are in danger of extinction; *C. trivalvis*, *C. grevei*, and *C. microfoliolata* are vulnerable.

Discussion and conclusion – Human activities including wood use and burning are the main pressures contributing to the depletion of species. As regards their conservation status, *Cedrelopsis* species are actually in an intermediate level between the categories “vulnerable” (VU) and “critically endangered” (CR). Managing their populations and habitats requires effective participation of key players.

Key words – *Cedrelopsis*, Katrafay, Madagascar, Rutaceae, ecology, IUCN conservation status.

Introduction et méthode – *Cedrelopsis* (Rutaceae), communément appelé Katrafay, est un genre endémique de Madagascar comprenant huit espèces d'arbres et d'arbustes qui poussent sur différents types de substrat et dans des écosystèmes primaires et/ou modifiés. Ces espèces font parties des plantes les plus exploitées et à usage multiple. Une évaluation écologique a été effectuée afin de comprendre les pressions et menaces qui pèsent sur les populations de *Cedrelopsis* et de définir leurs statuts de conservation ainsi que d'établir la stratégie de gestion durable.

Résultats-clés – Environ 65 à 100% de sous populations de *Cedrelopsis* se trouvent dans des sites qui n'ont aucune mesure de conservation appropriée. L'exploitation irrationnelle et la perte des habitats constituent une forte menace. *C. procera* est en danger critique d'extinction; *C. gracilis*, *C. longibracteata*, *C. ambanjensis* et *C. rakotozafyi* sont en danger d'extinction; *C. trivalvis*, *C. grevei* et *C. microfoliolata* sont vulnérables.

Discussion et conclusion – Les activités anthropiques incluant l'exploitation des bois et les feux constituent les principales pressions contribuant à la raréfaction des espèces de *Cedrelopsis*. En ce qui concerne leurs statuts de conservation, les espèces de *Cedrelopsis* sont actuellement à un niveau intermédiaire entre les catégories “vulnérables” (VU) et “en danger critique” (CR). La gestion de leurs populations et de leurs habitats naturels impose la participation effective des acteurs environnementaux.

INTRODUCTION

Parmi les plantes endémique de Madagascar, *Cedrelopsis* – communément appelé Katrafay – est utilisé à des fins diverses et variées (remède traditionnel, bois de construction et d'ébénisterie, bois de chauffage et de charbon, huile essentielle, etc.). De la famille des Rutaceae sensu lato (Razafimandimbison et al. 2010), ce genre comprend huit espèces dont *C. ambanjensis* J.-F.Leroy, *C. gracilis* J.-F.Leroy, *C. grevei* Baillon, *C. longibracteata* J.-F.Leroy, *C. microfoliolata* J.-F.Leroy, *C. procera* J.-F.Leroy, *C. rakotozafyi* Cheek & Lescot et *C. trivalvis* J.-F.Leroy. Il fait partie des composantes floristiques importantes des forêts sèches de l'Ouest et du Sud de Madagascar. Il est également dans les forêts littorales, les forêts denses humides de l'Est, les forêts denses sèches caducifoliées (Ouest) et les fourrés xérophiles (Sud-Ouest), ainsi que les formations savanicoles malgaches, sur différents types de substrats (karst, sable, calcaire, sol ferrugineux, sol alluvionnaire). Les huit espèces de *Cedrelopsis* sont réparties dans plusieurs sites naturels sans statut ni mesures de protection ou de conservation appropriées. Les différentes formes d'utilisation des produits dérivés des différentes espèces de *Cedrelopsis* constituent des pressions sur ces populations. Leurs habitats sont menacés par les feux de brousse, la culture itinérante sur brûlis et l'exploitation for-

estière. Pourtant, ces espèces n'ont pas encore de statut de conservation précis suivant l'UICN (Raivoarisoa 1999).

Afin d'améliorer l'état de connaissance sur *Cedrelopsis* et la politique de conservation de ces plantes, des travaux de recherche ont été entrepris afin de décrire les caractéristiques écologiques des espèces et de leurs habitats; connaître la potentialité des différents habitats naturels; décrire la distribution biogéographique de ces espèces (sous populations et populations à l'intérieur et en dehors des Aires Protégées); et déterminer les statuts de conservation suivant l'approche UICN (1994, 2001) de ces espèces.

MATERIEL ET METHODES

Zones et sites d'étude

Les localités relevées sur les étiquettes des spécimens disponibles dans différents centres de références à Madagascar et/ou figurant dans la base des données TROPICOS ont permis de choisir les sites d'étude. Ces données sont projetées sur la carte de végétation (Du Puy et Moat 1996), la carte géologique (Besairie 1964) et la carte bioclimatique (Cornet 1974) par le logiciel Arc View 3.3. Les sites choisis répondent aux critères de représentativité en fonction de la nature du sol et de la structure de végétation et des caractéristiques écologiques. Ainsi, quatorze sites ont été visités et étudiés

Tableau 1 – Localisation des sites d'étude et habitats des espèces de *Cedrelopsis*.

Espèces	Sites d'étude	Latitude	Longitude	Type de végétation
<i>Cedrelopsis ambanjensis</i>	Bekaka (Ambanja)	13°43'58"S	48°29'33"E	Forêt humide
<i>Cedrelopsis gracilis</i>	Andranomena (Morondava)	20°09'53,1"S	44°26'33,6"E	Forêt sèche
	Tanambao (Morondava)	20°43'52,3"S	44°28'44"E	Forêt sèche
<i>Cedrelopsis grevei</i>	Ankarafantsika (Ampijoroa)	16°17'55,7"S	46°49'02,6"E	Forêt sèche
	Andranomena (Morondava)	20°09'05,6"S	44°23'03,3"E	Forêt sèche
	Tanambao (Morondava)	20°43'52,9"S	44°28'38,4"E	Forêt sèche
	Menarahaka (Ihosy)	22°32'31"S	46°31'09"E	Forêt sèche
	Manavy (Antanimora)	24°57'25"S	45°45'26"E	Fourré xérophile
	Ankariera (Tolagnaro)	24°58'06"S	46°38'01"E	Forêt sèche
<i>Cedrelopsis longibracteata</i>	Elandy (Tolagnaro)	24°52'06"S	47°00'13"E	Forêt humide
<i>Cedrelopsis microfoliolata</i>	Orangea (Antsiranana)	12°13'51"S	49°21'23"E	Fourré
	Montagne des Français	12°22'22"S	49°20'57"E	Forêt sèche
	Sahafary (Antsiranana)	12°35'54"S	49°25'50"E	Savane arbustive
	Ankarafantsika (Ampijoroa)	16°19'08,4"S	46°48'34,2"E	Forêt sèche
	Andranomena (Morondava)	20°09'05,6"S	44°23'03,3"E	Forêt sèche
<i>Cedrelopsis rakotozafyi</i>	Menarahaka (Ihosy)	22°32'31"S	46°31'09"E	Forêt sèche
	Ankariera (Tolagnaro)	24°58'06"S	46°38'01"E	Fourré xérophile
	Orangea (Antsiranana)	12°13'51"S	49°21'23"E	Forêt sèche
	Sahafary (Antsiranana)	12°35'54"S	49°25'50"E	Forêt sèche
<i>Cedrelopsis trivalvis</i>	Orangea (Antsiranana)	12°13'51"S	49°21'23"E	Fourré
	Sahafary (Antsiranana)	12°35'54"S	49°25'50"E	Savane arbustive
	Ankarana (Ambilobe)	12°59'03"S	49°09'19"E	Forêt sèche
	Bekaka (Ambanja)	13°43'58"S	48°29'33"E	Forêt humide
	Menarahaka (Ihosy)	22°32'31"S	46°31'09"E	Forêt sèche
	Sainte Luce (Tolagnaro)	24°45'47"S	47°10'21"E	Forêt humide
<i>Cedrelopsis procera</i>	Antongondriha (Sambava)	14°16'05"S	49°45'0"E	Forêt humide

(tableau 1) dont sept forêts sèches; trois forêts humides; trois fourrés et une savane arbustive. Ces sites sont représentatifs des types de formations végétales existants abritant les différentes espèces de *Cedrelopsis*.

Récolte de matériel végétal et collecte des données relatives à *Cedrelopsis*

A partir de la littérature disponible, des informations relatives à *Cedrelopsis* ont été relevées. Des herbiers ont été consultés dans les deux centres nationaux de référence TAN et TEF et aussi aux laboratoires du Centre National d'Application à la Recherche Pharmaceutique (CNARP) et du Département de Biologie et Ecologie Végétales, Faculté des Sciences, Université d'Antananarivo (DBEV). La localisation, les noms vernaculaires, l'écologie, la phénologie ainsi que les modes d'utilisation des produits dérivés de *Cedrelopsis* ont été relevés sur un formulaire préétabli. La variation des caractères et des aspects morphologiques de différents organes a été observée suivant la définition de Gift & Stevens (1997). La terminologie pour la description des états de caractères morphologiques, ainsi que la fiche de description morphologique ont été établies suivant Radford et al. (1974). La morphologie comparative consiste à identifier des groupes phénotypiques (Stace 1989).

Les études prospectives de la flore et de la végétation ont été menées dans chaque site. Une prospection a été effectuée pour définir la végétation appropriée tout en tenant compte des critères phytoécologiques (homogénéité relative de la physionomie et du groupe floristique et l'uniformité des conditions édaphiques apparentes) et la présence et l'abondance des espèces cibles. Les coordonnées géographiques ont été enregistrées à l'aide de Global Positioning System (GPS).

Etude de flore

Pour connaître l'aspect floristique de la formation végétale, la méthode de plateau subdivisé en plusieurs placettes selon Braun-Blanquet (1965) a été adoptée. Cette technique consiste à dénombrer et à inventorier les espèces présentes sur une surface de 50 × 20 m soit 1000 m², subdivisée en placettes de 10 × 10 m. Pour chaque placette ont été relevés les noms vernaculaires, l'abondance spécifique, la forme biologique (Aubréville 1970), le diamètre (cm) à la hauteur de poitrine (DHP) à 1,30 m au-dessus du sol, la hauteur maximale (m) atteinte par l'individu ligneux et la phénologie (floraison, fructification, feuillaison) de chaque espèce afin d'avoir la composition, la richesse et les caractéristiques floristiques du site étudié. Dans chaque plateau pour chaque espèce rencontrée, des échantillons d'herbiers de référence ont été confectionnés. Le maximum d'informations a été noté afin de caractériser les spécimens d'herbiers, en particulier les caractères non rencontrés à l'état sec comme la couleur, l'odeur, l'architecture des arbres, la dimension de la plus grande feuille. Par espèce, quatre échantillons d'herbiers ont été déposés respectivement dans deux herbiers nationaux TAN et TEF et également aux laboratoires d'herbiers du CNARP et du DEBV.

Dans chaque plateau, tous les individus régénérés (plantules, semis, jeunes plants) et semenciers des espèces de *Cedrelopsis* ont été dénombrés afin de décrire les différentes classes démographiques. L'évaluation des individus matures a été effectuée. La densité spécifique (D) est le nombre d'individus présents d'une espèce considérée par unité de surface (Dajoz 1975). Elle est exprimée par la formule de Brower et al. (1990) $D = N/P$ (N: nombre d'individus d'espèce présents; P: surface totale de la parcelle étudiée). L'estimation de la densité dans une sous-population permet d'estimer le nombre d'individus matures en appliquant la formule $N = A \times D$ (N: nombre d'individus matures dans la sous-population; A: surface de l'habitat approprié pour l'espèce; D: densité dans la sous-population).

Etude de la végétation

La physionomie de la végétation est caractérisée par sa structure verticale constituée par des strates (Gounot 1969). Ainsi, pour chaque végétation étudiée, la hauteur de chaque strate et les espèces constitutives de chaque strate ont été mentionnées. On peut aussi calculer la densité de troncs associés et selon Brower et al. (1990), cette densité D des plantes par hectare est donnée par la formule $D = 10.000/S$ (S étant la surface occupée par les ligneux (arbres, arbustes, etc.) associés et les espèces cibles). Elle est donnée par la formule:

$$S = \frac{(\sum d)^2}{n(n + n')}$$

D (troncs/hectare) = $10\,000 \times n(n+n') / (\sum d)^2$

d : distance entre l'espèce cible et les ligneux (arbres, arbustes, etc.) associés;

n : nombre total des ligneux (arbres, arbustes, etc.) associés;

n' : nombre des ligneux (arbres, arbustes, arbrisseaux, etc.) cibles étudiés.

Régénération naturelle de *Cedrelopsis*

D'après Allaby (1994), la régénération naturelle d'une espèce est définie comme le stade de développement de ses individus à partir du moment où ils sont dispersés jusqu'à leur disparition. Elle comprend la phénologie, la pollinisation et la dispersion des graines qui ont été notées par des observations directes. Pour cette étude, les individus régénérés se développant soit à partir des graines soit par de rejet ont été observés. Rothe (1964) a défini la régénération naturelle comme la capacité d'une plante de se reproduire à l'état naturel. La régénération naturelle est basée sur le procédé de comptage du nombre d'individus de régénération (jeunes et semis) et de semenciers à l'intérieur d'un relevé en notant le diamètre et la hauteur. La régénération d'une espèce est exprimée à partir du taux de régénération $TR = (IR/IS) \times 100$ (IR: nombre d'individus de régénération; IS: nombre d'individus semenciers).

Suivant la valeur du taux de régénération, trois cas peuvent caractériser le potentiel de régénération:

- (i) TR > 1000%: espèce à haut potentiel de régénération;
- (ii) TR compris entre 100 et 1000%: espèce à potentiel de régénération moyen;
- (iii) TR < 100%: espèce à faible potentiel de régénération.

Analyse de la structure démographique des espèces cibles

– La distribution des individus de chaque espèce en différentes classes de diamètre a été définie comme suit: I:]0–5] cm; II:]5–10] cm; III:]10–20] cm; IV:]20– 30] cm; V: > 30 cm.

Estimation des risques d’extinction du genre Cedrelopsis

– La méthode d’évaluation de la distribution spatiale des espèces étudiées a été faite en prenant les coordonnées géographiques de spécimens de chaque espèce lors de travaux d’études sur le terrain et celles de la base de données TROPICOS. Elle comprend deux étapes: l’élaboration et l’analyse de la carte.

Elaboration de la carte de distribution – Les coordonnées géographiques de chaque espèce ont été transférées sur un tableur (Excel) et converties dans une projection Laborde avant d’être intégrées sous le logiciel Arcinfo. Les points de distribution de chaque espèce ont été placés sur la carte de Madagascar sous ce logiciel Arcinfo.

Analyse de la carte de distribution – A partir de la carte ainsi obtenue, le nombre total des sous populations, l’aire d’occurrence, l’aire d’occupation, la présence et/ou l’absence des espèces étudiées dans les Aires Protégées et leur prédiction de déclin futur ont été déduits et évalués. Le déclin de la population vient de la réduction continue des individus matures ou semenciers. La prédiction du futur déclin est estimée ou évaluée en utilisant la formule proposée par Schatz (2001):

Déclin de la population (%)

=

nombre de sous-populations hors des aires protégées

nombre total de sous-populations (dans AP et hors AP)

× 100

Pour compléter ces informations, le risque d’extinction de *Cedrelopsis* a été évalué sur les critères de la Liste Rouge (UICN 1994 et 2001) pour les espèces végétales (niveau espèce et niveau habitat).

Etudes comparatives des différents aspects morphologiques

Les études comparatives des différents aspects morphologiques (nombre, disposition, dimension et forme de folioles) et des caractères reproducteurs des différentes espèces collectées ont été réalisées en laboratoire.

RESULTATS

La description botanique, le bilan floristique et les caractéristiques écologiques des habitats d’espèces cibles ont été précisés. Les différentes formes d’utilisation et les pressions qui s’exercent sur les ressources végétales ainsi que leur distribution géographique en fonction des facteurs phytogéographiques et écologiques ont été déterminées afin de pouvoir évaluer et définir leur statut de conservation.

Distribution de Cedrelopsis

Cedrelopsis existe dans les trois des quatre biomes de Madagascar: forêt sèche et savane arbustive de l’Ouest, forêt humide de l’Est, fourré xérophile et forêt sèche du Sud de Madagascar. Les différentes espèces de *Cedrelopsis* sont caractérisées par différents aspects morphologiques et écologiques. Ces huit espèces de *Cedrelopsis* se répartissent dans quatre types de bioclimat à savoir l’étage humide, l’étage subhumide, l’étage sec et l’étage subaride et s’observent sur différents types de substrats. Les caractéristiques écologiques des habitats des différentes espèces cibles sont résumées dans le tableau 2.

Formations humides

Forêt littorale – La forêt littorale de Sainte Luce (Tolagnaro) est un des sites d’études dans laquelle seule *C. trivalvis* a été rencontrée (tableau 1). Pour la richesse floristique on compte, 82,9% de Dicotylédones, 13,4% de Monocotylédones et 3,7% de Ptéridophytes et autres (appendice électronique 1). Les familles les mieux représentées sont les Salicaceae (huit espèces), les Euphorbiaceae (cinq espèces),

Tableau 2 – Caractéristiques écologiques des habitats des différentes espèces de Cedrelopsis.

Espèces	Bioclimat	Nature du substrat	Type de végétation	Altitude (m)
<i>Cedrelopsis ambanjensis</i>	Étage subhumide	Socle, grès d’âge crétacé	Forêt Humide	300–350
<i>Cedrelopsis gracilis</i>	Étage subaride	Sables consolidés	Forêt Sèche	10–127
<i>Cedrelopsis grevei</i>	Étage subhumide, sec et subaride	Socle, calcaires-marnes d’âge dano-montien, carapace sableuse, grès, sable non consolidé, calcaire tertiaire	Forêt Sèche et Fourré	0–900
<i>Cedrelopsis longibracteata</i>	Étage humide	Gneiss, leptynites, pyroxénites, cipolins, quartzites	Forêt Humide	200–800
<i>Cedrelopsis microfoliolata</i>	Étage subhumide, sec et subaride	Dune quaternaire, grès du crétacé	Forêt Sèche et Fourré	5–1000
<i>Cedrelopsis procera</i>	Étage subhumide	Gneiss	Forêt Humide	400–500
<i>Cedrelopsis rakotozafyi</i>	Étage sec	Dunes blanches grésifiées d’âge quaternaire	Fourré et Savane arbustive	0–325
<i>Cedrelopsis trivalvis</i>	Etage humide, subhumide et sec	Dune quaternaire, grès du crétacé	Forêt littorale, Forêt Humide, Forêt Sèche et Fourré	5–1500

les Fabaceae et les Rubiaceae (quatre espèces chacune). Quant à l'aspect physionomique et structural de végétation, la forêt littorale est formée par quatre strates bien distinctes (cf. appendices électroniques 2 & 3).

Forêts denses humides – La forêt dense humide de Bekaka (Sambirano, dans le nord) et celle de l'Elandy (Tolagnaro, dans le sud) ont été étudiées. Dans la forêt de Bekaka (Ambanja), *C. trivalvis* est présente. Par contre, *C. ambanjensis* n'a pu être trouvée. La dégradation quasi-totale de l'ancienne relique forestière existante est très marquée. *C. longibracteata* a été trouvée dans la forêt d'Elandy (Tolagnaro).

Les caractères floristiques des deux sites mentionnés sont résumés dans l'appendice électronique 1. Pour ces deux sites, la richesse floristique est très élevée à Elandy soit 80 espèces où la perturbation du milieu y est relativement faible. La famille des Rubiaceae est mieux représentée dans les deux sites avec six espèces à Bekaka et onze espèces à Elandy. Les forêts humides sont pluristrates avec des hauteurs maximales de 16 m dans le site de Bekaka et de 22 m dans celui d'Elandy. Les strates herbacées sont moins développées dans ces deux formations végétales.

Les aspects physionomiques et structuraux des forêts humides de Bekaka et Elandy sont donnés dans les appendices électroniques 2 & 3. La stratification de la végétation d'Elandy est relativement similaire à celle de Bekaka, mais la différence s'observe au niveau des espèces présentes et l'importance du taux de recouvrement de différentes strates.

Formations sèches

Forêts sèches caducifoliées – Parmi les sept sites étudiés, ceux d'Andranomena et d'Ankarafantsika sont les plus riches en espèces avec respectivement 71 et 70 espèces recensées. Le bilan floristique des sept sites étudiés est mentionné dans l'appendice électronique 1.

Les familles les mieux représentées sont les Euphorbiaceae (onze espèces), les Fabaceae (six espèces) et les Rubiaceae (quatre espèces).

A Sahafary, les familles les mieux représentées sont les Fabaceae (sept espèces), les Euphorbiaceae et les Rubiaceae (cinq espèces chacune).

A Ankarana, les familles les mieux représentées sont les Fabaceae (sept espèces) et les Euphorbiaceae (quatre espèces).

A Ankarafantsika, les familles les mieux représentées sont les Fabaceae (neuf espèces) et les Euphorbiaceae (sept espèces).

A Andranomena, les familles les mieux représentées sont les Fabaceae (onze espèces), les Euphorbiaceae (sept espèces) et les Rubiaceae (quatre espèces).

A Tanambao, la famille des Fabaceae est la mieux représentée (neuf espèces).

A Menarahaka, les familles les mieux représentées sont les Euphorbiaceae (cinq espèces), les Fabaceae et les Rutaceae (quatre espèces chacune).

Sur le plan physionomique, les forêts sèches étudiées sont formées de plusieurs strates bien distinctes. Leurs données structurales sont données dans les appendices électroniques 2 & 3. En général, le taux de recouvrement de chaque

strate, le recouvrement et la hauteur de canopée des espèces varient d'une station écologique à l'autre et les arbres ayant une hauteur supérieure à 10 mètres sont relativement rares. Cela est dû à l'exploitation sélective ayant affecté les différents sites étudiés.

Fourrés

Les fourrés d'Orangea, d'Antanimora et d'Ankariera ont été étudiés (tableau 1). *C. microfoliolata*, *C. rakotozafyi* et *C. trivalvis* ont été répertoriées à Orangea; *C. grevei* à Antanimora et *C. grevei* et *C. microfoliolata* à Ankariera. Les caractères floristiques des trois sites étudiés sont présentés dans l'appendice électronique 1.

A Orangea, les familles les mieux représentées sont les Fabaceae (onze espèces), les Malvaceae (six espèces), les Apocynaceae et les Euphorbiaceae (cinq espèces chacune), et les Loganiaceae (quatre espèces).

A Antanimora, les familles les mieux représentées sont les Euphorbiaceae (six espèces), puis les Burseraceae, les Didieraceae, les Fabaceae et les Rubiaceae (trois espèces chacune).

A Ankariera, les familles les mieux représentées sont les Fabaceae (17 espèces), les Euphorbiaceae et les Malvaceae (huit espèces chacune), et les Brassicaceae (cinq espèces).

Le fourré d'Ankariera possède une richesse floristique importante (96 espèces enregistrées), qui est différente de celles de sites d'Antanimora et d'Orangea. Par contre de nombreuses espèces sont communes dans les deux derniers sites. Les espèces suivantes ont été rencontrées: *Azima tetracantha*, *Euphorbia leucodendron*, *Operculicarya decaryi*, *Quivisianthe papinae*.

Ces trois sites présentent des formations végétales à strates confuses et inextricables. Les caractéristiques structurales de ces types de végétation sont mentionnées dans les appendices électroniques 2 & 3.

Savane arbustive (Secteur Nord)

La savane de Sahafary (Antsiranana) où se trouve *C. rakotozafyi* présente 24 espèces, réparties dans 24 genres et 22 familles. Les informations sur la flore sont résumées dans l'appendice électronique 1. La végétation ne présente pas de strate bien définie, mais on peut distinguer une strate herbacée, continue avec un taux de recouvrement global de 90% (appendice électronique 2) et constituée essentiellement par *Heteropogon contortus* parsemée des arbustes qui ne dépassent pas 5 m de hauteur. On y rencontre plusieurs espèces (appendice électronique 3).

Abondance et densité de *Cedrelopsis* dans les différents sites

L'abondance numérique des espèces de *Cedrelopsis* varie d'une végétation à l'autre selon les caractères climatiques et édaphiques.

C. gracilis: 90 individus matures ont été trouvés sur 2,2 ha dans deux sites;

- C. grevei*: 1619 individus matures ont été trouvés sur 8,5 ha dans six sites;
- C. longibracteata*: 14 individus matures ont été trouvés sur 1,4 ha dans un seul site à Elandy;
- C. microfoliolata*: 484 individus ont été trouvés sur 13 ha dans sept sites;
- C. rakotozafyi*: 183 individus ont été trouvés sur 7,2 ha dans 2 sites;
- C. trivalvis*: 111 individus ont été trouvés sur 9,6 ha dans les 6 sites.

Pour l'ensemble des sites d'études, *C. grevei* et *C. gracilis* sont les plus abondantes.

Phénologie et dispersion de diaspores

En se basant sur la période de floraison maximale, trois groupes peuvent être mis en évidence:

- Groupe 1: une floraison toute l'année, cas de *Cedrelopsis grevei*;
- Groupe 2: une période optimale de floraison en saison sèche au mois d'octobre (*C. longibracteata* et *C. trivalvis*);
- Groupe 3: une période optimale de floraison en saison humide de novembre à décembre (*C. gracilis*, *C. microfoliolata*, *C. procera* et *C. rakotozafyi*).

En ce qui concerne la phénologie de *C. ambanjensis*, *C. gracilis*, *C. longibracteata*, *C. procera* et *C. rakotozafyi*, les données disponibles ne sont pas suffisantes pour caractériser de façon précise leur période de floraison et de fructification.

Toutes les espèces de *Cedrelopsis* présentent des fruits secs capsulaires déhiscent avec des graines ailées d'où la dissémination de diaspores est assurée par le vent ou anémochorie.

Potentialité de régénération de *Cedrelopsis*

C. gracilis, *C. grevei*, *C. longibracteata*, *C. microfoliolata*, *C. rakotozafyi* et *C. trivalvis* ont deux types de régénération naturelle. La régénération se fait à partir de la graine ou par voie sexuée et l'autre par voie asexuée ou végétative, après une coupe de la tige, les espèces sont capables de donner des rejets. De plus lorsque les arbres vieillissent, un pied pourra donner un rejet lequel remplacera plus tard le pied-mère. Ce cas est également observé pour les espèces *C. grevei* et *C. microfoliolata*. Ces deux types de rejet présentent une différence morphologique du point de vue dimension et croissance. Le taux de régénération de chaque espèce est résumé dans l'appendice électronique 4. Ce taux de régénération varie durant toute l'année en fonction de la période d'observations et de la période de germination ainsi que les sites d'études. *C. trivalvis* (Sainte Luce), *C. grevei* (Antanimora et Menarahaka) ont de taux de régénération très élevés. Par contre, ce taux de régénération est presque nul pour *C. trivalvis* (Menarahaka).

Structure démographique de *Cedrelopsis*

La répartition des individus par classe de diamètre pour les différentes espèces de *Cedrelopsis* permettant d'estimer les pressions et menaces sur les espèces et/ou leurs habitats est résumée dans l'appendice électronique 5. La distribution des individus de *C. gracilis* à Andranomena a une allure régulière avec une absence d'individus ayant de diamètre supérieur à 20 cm. Ceci indique une exploitation fréquente de cette espèce liée à la dégradation de l'habitat. La régénération de populations de *Cedrelopsis* est en général bonne. Tous les individus qui ont de diamètre supérieur à 5 cm (dimension voulue pour toutes sortes d'exploitation) deviennent rares. Ce fait indique entre autres, la pression liée à la coupe de bois. A Elandy, la distribution des individus de *C. longibracteata* présente une allure irrégulière du fait de l'absence de trois classes de diamètre suivantes: classes II, IV et V. Cette

Tableau 3 – Récapitulatif des données sur la distribution géographique de *Cedrelopsis*.

Espèces	Répartition par domaine: Humbert (1955)	Aire d'occurrence (EOO) (km²)	Aire d'occupation (AOO) (km²)	Nombre total des sous populations	Nombre des sous populations dans les APs	Prédiction du futur déclin (%)
<i>Cedrelopsis ambanjensis</i>	Sambirano	1083,11	27	03	1	66,67
<i>Cedrelopsis gracilis</i>	Ouest	18	18	02	0	100
<i>Cedrelopsis grevei</i>	Ouest, Sud et Sud Ouest	436505	873	88	10	88,63
<i>Cedrelopsis longibracteata</i>	Est	2616,68	27	02	1	50
<i>Cedrelopsis microfoliolata</i>	Ouest, Sud et Sud Ouest	330339	243	27	4	85,18
<i>Cedrelopsis procera</i>	Est	9	9	1	0	100
<i>Cedrelopsis rakotozafyi</i>	Ouest (Secteur Nord)	228,804	36	04	0	100
<i>Cedrelopsis trivalvis</i>	Est, Sambirano, Ouest, Sud Ouest	408092	180	17	02	88,23

Tableau 4 – Evaluation du risque d’extinction des espèces de *Cedrelopsis* étudiées.

nT: nombre total de sous populations des espèces cibles; n’T: nombre de sous populations des espèces cibles en dehors des Aires Protégées; FDH: Forêt Dense Humide; FSC: Forêt Sèche Caducifoliée; FL: Forêt littorale.

Critères	<i>Cedrelopsis ambanjensis</i>	<i>Cedrelopsis gracilis</i>	<i>Cedrelopsis grevei</i>	<i>Cedrelopsis longibracteata</i>	<i>Cedrelopsis microfoliolata</i>	<i>Cedrelopsis procera</i>	<i>Cedrelopsis rakotozafyi</i>	<i>Cedrelopsis trivalvis</i>
Type de végétation	FDH	FSC	FSC, Fourré Sec, Bush xérophile,	FDH	FSC, Fourré Sec	FDH	Fourré, Savane	FL, FDH, FSC
Abondance numérique	-	90	1619	14	484	-	183	111
TR(%)	-	199,99	2555,50	1100	802,39	-	438,09	1685,55
Aire d’occurrence (km²)	1083,11	18	436505	2616,68	330339	9	228,804	408092
Aire d’occupation (km²)	27	18	873	27	243	9	36	180
nT	3	2	88	2	27	1	4	17
n’T	2	2	78	1	23	1	4	15
Futur déclin (%)	66,67	100	88,63	50	85,18	100	100	88,23
Utilisation	Oui	Oui	Oui	Oui	Oui	-	Oui	Oui
Statuts UICN proposés	EN B1ab (i, ii, iii, iv) + 2ab (i, ii, iii, iv)	EN B1ab (i, iii, iv)	VU B2b (ii, iii)	EN B1ab (i, ii, iii, iv) + 2ab (i, ii, iii, iv)	VU B2ab (ii, iii, iv)	CR B1ab (i, ii, iii, iv) + 2ab (i, ii, iii, iv)	EN B1ab (i, ii, iii, iv) + 2ab (i, ii, iii, iv)	VU B2ab (ii, iii)

irrégularité est due à l’exploitation abusive de ses écorces après l’abattage effectif des individus.

La distribution des individus de *C. microfoliolata* est caractérisée par une allure plus ou moins régulière. Les individus qui ont de diamètre supérieur à 30 cm sont présents uniquement dans le site de la Montagne des Français. L’éloignement et le fait que le site soit très difficile d’accès ont permis sa conservation. Quant à *C. rakotozafyi*, dans le site d’Orangea, on peut déduire des résultats la surexploitation de l’espèce pour la construction et la fabrication de charbon. A Sahafary, les individus de diamètre supérieur à 10 cm sont rares.

La distribution des individus de *C. trivalvis* a une allure régulière dans les sites d’Orangea, Sahafary, Ankarana, Bekaka et Sainte Luce. Les rares individus de diamètre supérieur à 30 cm ne s’observent qu’à Sahafary et à Ankarana. A Menarahaka, on note une distribution irrégulière due certainement au passage fréquent de feux de brousse.

Pressions et menaces sur les espèces de *Cedrelopsis*

Les principales menaces qui pèsent sur les espèces étudiées sont les exploitations par diverses modes d’utilisation des ressources en bois (cf. appendice électronique 6A) ainsi que la perte et la dégradation des habitats naturels. L’importance de l’exploitation dépend de l’accessibilité et surtout du statut de conservation de sites. La présence de gestionnaires de sites ne peut pas parfois freiner les besoins des communautés locales en ressources végétales et en général des différentes formes de pressions persistent. Les différentes formes de pressions et menaces liées à l’utilisation des ressources sont résumées dans l’appendice électronique 6B. L’extraction d’huile essentielle de *Cedrelopsis* n’est pas observée sur le terrain, pourtant l’huile essentielle de Katrafay est vendue sur les marchés locaux à Madagascar voire à l’international.

Prédiction du futur déclin des espèces de *Cedrelopsis*

Les aires d’occurrence varient d’une espèce à l’autre (cf. tableau 3), d’une superficie très restreinte (9 km²) à une superficie assez large (436505 km²). Nos résultats montrent un taux de futur déclin ≤ 50% pour *C. longibracteata*; et un taux > 50% pour six autres espèces sur les sept que nous avons pu collecter dont *C. ambanjensis* (66,7%), *C. microfoliolata* (85,2%), *C. trivalvis* (88,2%), *C. grevei* (88,6%), *C. gracilis* (100%), et *C. rakotozafyi* (100%). Ainsi, compte tenu de ces données, les espèces de *Cedrelopsis* sont classées dans les catégories suivantes selon les statuts de conservation de l’IUCN: En Danger Critique d’Extinction (CR) pour le cas de *C. procera*; En Danger d’Extinction (EN) pour *C. ambanjensis*, *C. gracilis*, *C. longibracteata* et *C. rakotozafyi*; Vulnérable (VU) pour *C. grevei*, *C. microfoliolata* et *C. trivalvis* (cf. tableau 4).

DISCUSSION

Caractères morphologiques de *C. grevei* et *C. trivalvis*

C. grevei – Des variations morphologiques ont été observées chez certains individus d’une même espèce rencontrée à Ankarafantsika (nord ouest) et Ankariera (sud et faible pluvio-

métrie). Ces variations sont particulièrement marquées au niveau de taille et de forme ainsi le nombre de paires de folioles de feuilles. Les feuilles peuvent atteindre 22×13 cm généralement avec huit paires de folioles à Ankarafantsika contre 12×6 cm avec six paires à Ankariera. Ces caractères pourraient être dûs à de changement des facteurs écologiques et climatiques. En somme, il n'y a pas de critères morphologiques spécifiques permettant de séparer des morpho-espèces et jusqu'à maintenant cette espèce est considérée comme espèce polymorphe.

C. trivalvis – Les caractères morphologiques distinctifs sont observés au niveau de la taille des individus, la dimension de feuille, le nombre de paires de folioles et la présence ou l'absence de poils sur la nervure de la face inférieure de feuille. Les individus trouvés dans les forêts sèches ont des houppiers très développés par rapport à la hauteur du fût mais contrairement aux individus qui poussent dans les forêts humides. Pour le site de Menarahaka, les individus présentent des petites feuilles de $4-5 \times 1-2$ cm et avec 4-5 paires de folioles. Il y a des poils dans la nervure médiane. Alors que dans les autres sites d'études, les feuilles peuvent atteindre $8-16 \times 4-6$ cm avec 5-10 paires de folioles et caractérisées par de nervures glabres. Donc cela nécessite une étude plus élaborée et approfondie par des méthodes cytogénétiques et d'autres. Les informations relatives aux aires d'occupation (AOO) et d'occurrence (EOO) sont probablement sous-estimées pour certaines espèces à répartition biogéographique relativement large à cause d'un certain nombre de localités ou sites non prospectés. Le manque d'informations précises sur le nombre d'individus semenciers matures de différentes espèces étudiées constituerait également une lacune sur la définition exacte de leurs statuts de conservation. Et en général, la potentialité de régénération des différentes espèces de *Cedrelopsis* est bonne, mais leur vitesse de croissance et de développement est relativement lente.

Le génotypage de *C. grevei* et *C. trivalvis* de différents sites permettra de réviser la taxonomie de ces espèces.

Prédiction du futur déclin des espèces de *Cedrelopsis*

Selon Humbert (1955), les espèces de *Cedrelopsis* sont présentes dans tous les domaines phytogéographiques de Madagascar, à l'exception du domaine du centre et des hautes montagnes. Cependant, les résultats mentionnés ont mis en évidence le futur déclin qu'en moins de trois prochaines décennies de ce genre *Cedrelopsis*.

Stratégie de conservation des espèces étudiées

Cette étude a permis de connaître l'état actuel de *Cedrelopsis* à Madagascar, avec ces espèces qui sont vulnérables et relativement menacées à cause de leurs utilisations irrationnelles et la dégradation de leurs habitats naturels. Des mesures alternatives s'avèrent nécessaires pour assurer la pérennisation de ces espèces aussi bien à l'intérieur qu'à l'extérieur de leurs habitats naturels. Pour cela, on peut suggérer deux recommandations conformément à la stratégie de conservation à Madagascar:

Conservation in situ – Les mesures à entreprendre se focaliseront sur la conservation de ces habitats naturels sous forme d'une gestion d'Aires Protégées.

Conservation ex situ – Cette approche est indispensable pour les espèces qui risquent de s'éteindre dans le milieu naturel en conservant les graines des espèces dans une banque de graines pour une éventuelle restauration de populations.

CONCLUSION

Les résultats obtenus ont mis en évidence que les espèces de *Cedrelopsis* étudiées s'observent dans des formations forestières primaires et certaines formations végétales modifiées. Les aspects physiologiques et structuraux de végétation étudiée ont montré que les espèces de *Cedrelopsis* sont forestières mais elles peuvent être observées également dans les formations végétales fortement dégradées. A Sahafary, l'habitat de *C. rakotozafyi* est une formation herbeuse. En ce qui concerne la distribution de différentes espèces, *C. procera* est une espèce strictement localisée. *C. ambanjensis* n'ayant pas pu retrouver dans l'ancienne zone d'occupation. *C. gracilis*, *C. longibracteata* et *C. rakotozafyi* sont à distribution relativement restreinte. Actuellement, *C. grevei*, *C. microfoliolata* et *C. trivalvis* présentent encore une distribution large. Cependant, toutes les espèces de *Cedrelopsis* sont des plantes à usage multiple. Certaines modes d'utilisation représentent des sérieuses pressions et menaces pour certaines espèces de *Cedrelopsis*. L'évaluation du statut UICN des espèces de *Cedrelopsis* montre qu'elles sont classées dans trois catégories: "en danger critique d'extinction" (CR), "en danger d'extinction" (EN) et "vulnérable" (VU). De ce fait, la stratégie de conservation de ces espèces devrait être focalisée sur la gestion rationnelle de leurs populations et sur la conservation de leurs habitats naturels. Ainsi, des études complémentaires sont à faire sur *Cedrelopsis* notamment en phylogénie et en anatomie liée à la dendrochronologie.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible au format pdf sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> > SBB50 > dossier 584) et comprend: (1) bilan d'inventaire floristique dans les quatorze sites étudiés; (2) données structurales des quatorze sites étudiés; (3) données structurales sur la composition floristique des quatorze sites étudiés; (4) taux de régénération (TR) des espèces étudiées; (5) distribution des individus par classe de diamètre; et (6) utilisation des différentes espèces de *Cedrelopsis*, ainsi que différentes formes de pressions et menaces sur les espèces de *Cedrelopsis* et leurs habitats.

REMERCIEMENTS

Cette étude est réalisée grâce à la collaboration entre par le Département de Biologie et Écologie Végétales de l'Université d'Antananarivo, l'Université de Stockholm de Suède, le Centre National d'Application de Recherches Pharmaceutiques et Institut Pasteur de Madagascar, a été financée par le Ministère des Affaires Etrangères français via

le Projet Sud Expert Plantes numéro 347 (SEP 347 *Cedrelopsis* Madagascar). Nous tenons à exprimer nos vifs remerciements et notre profonde gratitude à tous ceux qui nous ont aidé à achever ce travail notamment à l'IRD-Madagascar, à Madagascar National Parks, à l'Université d'Antananarivo et au Ministère des Forêts et de l'Environnement de Madagascar.

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Manuscript received 31 Oct. 2010; accepted in revised version 11 Mar. 2013.

Communicating Editor: Elmar Robbrecht.



Biogeography and conservation status of *Phyllanthus* (Phyllanthaceae) in Madagascar

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Background – *Phyllanthus* is growing in a wide variety of habitats. In Madagascar the genus is found mainly in secondary vegetation, in different types of vegetation such as humid forest, dry forest, Tapia forest, dry spiny forest, littoral forest or sometimes on rocks in river beds. It occurs in all climatic regions and altitudinal zones of the island.

Results – The distribution of *Phyllanthus* of Madagascar is presented. Forty-seven of the 54 *Phyllanthus* species known in Madagascar are endemic. Madagascan *Phyllanthus* are grouped in two sets according to their ecological preference and distribution. The non-endemic species have mainly wide distributions and most of the endemic species have restricted distributions. The latter are generally confined to certain habitats and particular ecological conditions.

Conservation – Habitat loss due to human activities constitutes the principal threat to *Phyllanthus*. About 52% of *Phyllanthus* assessed are threatened. The results of the conservation assessments for the Madagascan *Phyllanthus* show that they occur in all of the threatened IUCN Red List categories from Critically Endangered to Vulnerable and the non-threatened categories Near Threatened and Least Concern as well as the Data Deficient category where the species are too poorly known to be assessed.

Key words – *Phyllanthus*, Phyllanthaceae, Madagascar, distribution, endemic, threat, assessment, IUCN Red List categories.

INTRODUCTION

Madagascar is an island unique in its highly diverse flora and fauna which show high levels of endemism. About 14,000 plant species are currently known for Madagascar, of which 91% are endemic to the island (Phillipson et al. 2006). Madagascar is also considered one of the World's main conservation hot spots by its biodiversity richness coupled with the degradation of its natural ecosystems. Currently natural vegetation such as forests occupies only 18% of its surface (Moat & Smith 2007) but most of the remaining vegetation is threatened. Therefore many species are likely to become extinct even before they are studied. *Phyllanthus* species might be among these plants.

Phyllanthus sensu lato is by far the largest genus in Phyllanthaceae, and one of the largest genera of the angiosperms. This paper is part of results of a recent taxonomic revision recognising nine subgenera, 54 species, including nine species to be described, and two infraspecific taxa of *Phyllanthus* in Madagascar (Ralimanana 2007, Ralimanana & Hoffmann 2011). Forty-seven of the known species are endemic to the island (Ralimanana 2007). *Phyllanthus* grows in a wide variety of habitats and some taxa are generally confined to certain habitats and particular ecological conditions

in Madagascar. Therefore some of them are more threatened by habitat loss than others.

Assessment of conservation status and trends of the biological diversity is one of the aims of the Convention on Biological Diversity (CBD 2001). This study was carried out to provide data about distribution and IUCN conservation status of Madagascan *Phyllanthus*. On the one hand data presented here are important for a Red Data List or a catalogue of threatened plants species production. On the other hand it provides information which is fundamental on biodiversity conservation planning and on the identification of sites where conservation actions should be taken in Madagascar. Only species which are validly published were assessed. Conservation status of new species found during this study will be published in another series of papers.

MATERIAL AND METHODS

This work is based on herbarium studies and fieldwork. Herbarium material of *Phyllanthus* was consulted mainly at the Royal Botanic Gardens, Kew (K), Muséum National d'Histoire Naturelle, Paris (P), Natural History Museum, London (BM), Linnean Herbarium, Stockholm (LINN) and in the national herbaria of Madagascar: Parc Botanique et

Zoologique de Tsimbazaza, Antananarivo (TAN) and Recherches Forestières et Piscicoles, Antananarivo (TEF).

All data on specimen labels were noted. For each species geographic coordinates were registered into an Access database. The accuracy of these coordinates was checked on maps. Sometimes old collections only show information about localities names where the specimens were collected. In these cases the Geonames gazetteer (<http://www.geonames.org>) was used in order to get coordinates. The coordinates in the database were analysed using GIS (Arc View 3.3) to prepare distribution maps for each species. Additional information about habitat was obtained by using different layers such as the vegetation and geology maps of Du Puy & Moat (1996), the vegetation map produced by Faramalala (1988) and Madagascar's bioclimates maps (<http://www.mobot.org/mobot/research/madagascar/gazetteer/>).

The conservation status of each species was assessed by using Conservation Assessment tools developed in the Royal Botanic Gardens, Kew (<http://www.kew.org/science-research-data/kew-in-depth/gis/resources-and-publications/tools/cat/index.htm>). Conservation status is based on calculating the extent of occurrence and the area of occupancy using GIS, and applying IUCN Red List categories and criteria (IUCN 2001).

Particular consideration is made for *Phyllanthus nummulariifolius* Poir. because one of its infraspecific taxa is endemic to Madagascar and threatened; and the other one is non-endemic and common in tropical areas. The results of the conservation assessments have been validated by the Groupe des Spécialistes des Plantes Malgaches (GSPM) for inclusion on the Madagascan plants Red List.

Collecting fieldtrips were carried out in different areas of Madagascar. Field observations were mainly focused on species descriptions, habitat, population size and threat. Information about species use is sometimes provided by the local guides or villagers.

RESULTS

Distribution and ecology

The level of endemism of *Phyllanthus* species is high for Madagascar. Eighty-seven per cent of *Phyllanthus* species are endemic to the island; they are found in different vegetation types such as humid forest, dry forest, dry spiny forest, Tapia forest, littoral forest, wooded grassland or in particular habitats like rocks in river beds. This genus occurs in all climatic regions and altitudinal zones of Madagascar from 0 to 2,300 m.

Analysis of the data has shown two main groups in relation to distribution: species with wide distributions which are mostly represented by non-endemic species; and those with restricted distributions, all endemic to Madagascar.

Of the 54 species, 47 species are endemic to Madagascar, three species are paleotropical (*Phyllanthus maderaspatensis* L., *P. nummulariifolius* Poir., and *P. tenellus* Roxb.), two species are pantropical (*P. amarus* Schumacher & Thonn., *P. urinaria* L.), one species occurs in both the Mascarene islands and Madagascar (*P. casticum* P.Willemet), and one species

is found in Madagascar and also in the Comoros and Seychelles (*P. pervilleanus* (Baill.) Müll.Arg.).

The species with a more restricted distribution are generally confined to certain habitats and particular conditions (electronic appendix 1). Some examples of the latter are given below:

Species of high montane areas – These species are found in the high montane zones of the central domain of Madagascar at altitudes of 1,300–2,300 m. The vegetation is an evergreen forest with canopy height declining with increasing elevation. The frequency of clouds generates high humidity in this kind of habitat.

Phyllanthus ankaratrae (Leandri) Petra Hoffm. & McPherson, *P. humbertii* (Leandri) Petra Hoffm. & McPherson, *P. lichenisilvae* (Leandri) Petra Hoffm. & McPherson, *P. marojejiensis* (Leandri) Petra Hoffm. & McPherson, *P. oreichtitus* Leandri, *P. perrieri* (Leandri) Petra Hoffm. & McPherson, and *P. sambiranensis* Leandri are only found in these higher montane ranges. All these species belong to the subgenus *Gomphidium* (Baill.) G.L.Webster.

Species of littoral forest in the eastern domain of Madagascar – This habitat is only found in a narrow and now discontinuous strip of Madagascar's eastern coast from Vohemar in the North to Tolagnaro in the South-East. It is a stratified and evergreen forest, with a low to high canopy (6–16 m) dominated by medium to large trees. The two-layered understorey is rich in treelets, shrubs and herbaceous plants.

Phyllanthus cryptophilus Müll.Arg., *P. gordonii* sp. ined., and *P. madagascariensis* Müll.Arg. var. *madagascariensis* are typical of littoral forest and they do not occur in any other habitats in Madagascar.

Species of Uapaca forest in the central domain of Madagascar – *Uapaca* forest is an open and stratified vegetation which is rich in herbaceous and shrubby plants. *Phyllanthus vakinakaratrae* Leandri is only found in this type of vegetation.

Species of quartzitic massif in the central domain of Madagascar – *Phyllanthus betsileanus* Leandri subsp. *betsileanus* grows only in the massif quartzitic of Itremo and Ibity in the central domain of Madagascar. Elevation in these areas is between 1,300 and 1,650 m. Analysis with Maxent has shown that digital elevation model (35.9%) and geology (20.4%) are the most important environmental variables which influences distribution of this taxon.

Rheophyte species – *Phyllanthus bernierianus* Baill. ex Müll.Arg. and *P. rangoloakensis* Leandri only grow on rocks in river beds or streams of the Eastern domain of Madagascar.

Species of dry and subarid zones of the western and south western domains of Madagascar – Dry forests and dry spiny forests are typical of these domains. For instance *Phyllanthus bojerianus* Müll.Arg., *P. isomonensis* Leandri, *P. mananarensis* Leandri, *P. multiflorus* Poir., *P. obdeltophyllus* Leandri occur only in dry and subarid habitat types.

Conservation

Thirty-one *Phyllanthus* species have already been validated by GSPM for the IUCN Red List in 2008. Since then additional data have been obtained so some updates are given here. The conservation status of 44 taxa are presented in this paper.

Among the 44 taxa assessed: two are Critically Endangered (EN), eleven are Endangered (EN), eleven are Vulnerable, four are Near Threatened (NT) and fourteen of Least Concern (LC).

Some species are endemic but they are rated as LC because they are widespread and are sometimes abundant. In addition such species may be found in one or more protected areas. Two taxa are known only from the type collection, or without a precise indication of the locality of collection, but no field verification has yet been done. Therefore these are rated as Data Deficient (DD).

Collecting for traditional medicine does not present any threat to *Phyllanthus* because common species such as *P. amarus*, *P. casticum* and *P. matitanensis* Leandri are mostly used. Concerning Madagascan *Phyllanthus* the main threat is habitat loss from cut and slash cultivation (tavy), fires, charcoal production and sometimes mining exploitation. The endemic species and those occurring only in a particular restricted habitat present a high risk of extinction. The results presented here show that about 52% are threatened. Details of the conservation assessment are summarized in electronic appendices 2, 3 & 4.

DISCUSSION

The plants of Madagascar have been the subject of taxonomic study for more than two centuries and still remain relatively unknown, given the island's remarkable levels of habitat heterogeneity and floristic diversity compared to its size (Gautier & Goodman 2003). It is generally accepted that the high level of angiosperm endemism at specific level is associated with the long-term isolation of Madagascar through geological time. In addition to the history, contemporary environmental factors such as climate, topography and edaphic factors play important roles in the diversity and distribution of plants species in Madagascar. The island is composed of a wide variety of bedrock and soil types, as well as varied topography (Du Puy & Moat 1996, Battistini 1996).

As Madagascar is separated by only 400 km from the eastern African coast, the affinity of its *Phyllanthus* species with those of Africa could be expected to be high. However, some remarkable differences are noted between Madagascar and Africa. The comparison of our results with Brunel's (1987) shows that only pantropical species such as *Phyllanthus amarus*, *P. maderaspatensis*, *P. nummulariifolius*, *P. urinaria*, and *P. tenellus* are common for the two regions. This suggests that the difference in *Phyllanthus* species is linked to the early separation of Madagascar from Africa. This separation started during the late Jurassic period (165 MYA). Madagascar arrived at its current position around 121 MYA (Rabinowitz et al. 1983).

Gomphidium is an infra-generic division within *Phyllanthus* that is recognized in Madagascar. With 49 species

(Schmid 1991), New Caledonia is the world centre of diversity for *Gomphidium*. Smaller numbers of species of this sub-genus are also found in Fiji, India, and Australia. In these areas *Gomphidium* grows in habitats with altitudes between 200 and 1,000 m. For Madagascar, *Gomphidium* is represented by ten species with disjunct distributions. They only occur in the high mountains such as Ankaratra, Andringitra, Marojejy and Tsaratanana, reaching 2,137–2,876 m in altitude. In Africa, Brunel (1987) failed to find any representatives of *Gomphidium* when he studied the *Phyllanthus* of tropical Africa, including on the Kilimanjaro, the continent's highest point. It is thought that the angiosperms were not present on Madagascar during the slow drift to its current position between 165 and 121 MYA (Schatz 1996). Given the predicted positions of Gondwanan land masses during the initial Cretaceous radiation of the angiosperms, between the time of arrival of Madagascar at its current position and the time separation of Greater India from Madagascar 88 MYA (Storey et al. 1995), we may assume that *Gomphidium* reached Madagascar by long distance dispersal from the East.

Global climate patterns are influenced by latitude and local geography (Jury 2003). For Madagascar, climatic conditions are determined mainly by geographic position, relief and the southeastern trade wind or Alizé (Donque 1975). Madagascar presents an East-West topographic asymmetry. The land rises abruptly from the east coast to reach the central high plateau, which declines gradually to the west and the southwest over the western sedimentary fringe (Wells 2003). This geomorphology has an impact on rainfall across the island. The eastern region is wetter than the western and southwestern regions at all times of the year, due to the orographic rain as the southeastern trade winds meet the steep eastern mountain ranges. In addition, there is also a north-south climatic gradient, which is most marked along the west coast, from the northwestern humid forest to the south western semi desert. All of these factors contribute in the distribution of the Madagascan flora. *Phyllanthus* is not an exception as, for example, some species are restricted to the dry and subarid zones of western and south western domains of Madagascar, whereas others only occur in the humid areas of the eastern domain.

Some *Phyllanthus* species are entirely restricted to a particular habitat; for example, the taxa occurring only in the littoral forests. Despite their small land surface, littoral forests have distinctive floras and high species richness and diversity (Rabevohitra et al. 1998). Only 274 km² remain (about 0.05% of Madagascar surface), but the littoral forests supports 13% of Madagascar's total native flora and 25% of the species present are littoral forest specialists (Moat & Smith 2007). Littoral forests are one of the most threatened vegetation types of Madagascar, mostly due to charcoal production and shifting agriculture (Rabevohitra et al. 1998). Littoral forests deserve the highest conservation priority and it is critical that a concerted effort is made to conserve the few remaining fragments.

Loss of biodiversity is a growing problem in the world, but it is a critical problem in Madagascar. As in most tropical areas, deforestation is the main threat to plant and animal species in Madagascar. Efforts are being made to reduce the

loss by developing programmes and strategies for conservation such as the new system of protected areas.

The protected area system in Madagascar was largely designed using animal data (Kremen et al. 2008, Rebioma 2011). We found that 52% of the *Phyllanthus* of Madagascar are threatened with extinction and they are found across Madagascar in all major vegetation types. Results presented here show the threat to biodiversity and the imperative for conservation are greater than ever.

SUPPLEMENTARY DATA

Supplementary material is available in pdf at the Supplementary Data Site of publications from the National Botanic Garden of Belgium (<http://www.nbgpublisher.be> > SBB50 > folder 522) and consists of the following: (1) a map of Madagascar showing some *Phyllanthus* species with restricted distribution; (2) a survey of taxa listed in the categories Critically Endangered (CR), Endangered (EN) and Vulnerable (VU); (3) a survey of taxa listed in the categories Near Threatened (NT) and Least Concern (LC) and (4) a survey of taxa listed in the categories Data Deficient (DD).

ACKNOWLEDGEMENTS

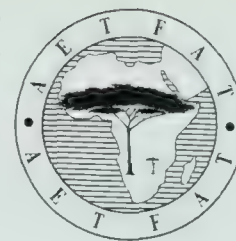
I would like to thank the Friends of Kew, the Bentham Moxon Trust and the Royal Botanic Gardens, Kew, who supported this study. I also thank the staff of the following herbaria for placing at our disposal herbarium material of *Phyllanthus*: British Museum of Natural History (BM), Royal Botanic Gardens, Kew (K), Linnean Society (LINN), Muséum National d'Histoire Naturelle, Paris (P), Département Flore, Parc Botanique et Zoologique de Tsimbazaza (TAN), Département des Recherches Forestières et Piscicoles, Antananarivo (TEF). My thanks go to Madagascar National Parks (MNP) and the Direction Générale de l'Environnement et Forêts (DGEF) for the research and collects permits. I particularly thank Pr C. Rajeriarison (DBEV) and Dr Petra Hoffmann (K) for the supervision during my study.

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Manuscript received 20 Sep. 2010; accepted in revised version 2 Mar. 2012.

Communicating Editor: Thomas Haevermans.



A participatory approach for plant conservation in Madagascar

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Context – Madagascar's natural habitats are a home of about 12,000 to 14,000 plant species and its forests provide ecological goods and services that are crucial for the survival of the Malagasy people and their economic development. Improvements are being made to agricultural production through developing better water sources, providing wild food and energy for cooking, and promoting income-generating opportunities. These goods and services are, however, threatened by the country's alarming rate of deforestation and loss of floristic biodiversity.

Methods – to improve the preservation of forest ecosystems, a participatory approach has been adopted by Conservation International's Madagascar Program and its partners to conduct three main activities: (a) the definition of Key Biodiversity Areas for Plants, (b) biodiversity knowledge management, and (c) creation of new Protected Areas. Technical and financial support has been provided to improve the participation of various national and international partners.

Key results – Eighty-nine Key Biodiversity Areas for Plants were identified based on threatened plant species, knowledge has been improved on the conservation status of some plant species, about 1848 plant species were recently assessed by the Madagascar Plant Specialist Group using the IUCN Red List criteria, biodiversity databases and networks are available at national and international levels, and an area of approximately 7.2 M hectares representing various ecosystems have been protected, which include most of plant threatened species.

Key words – Biodiversity, conservation, management, protected areas, ecosystem services, Key Biodiversity Areas, participatory approach, Madagascar.

INTRODUCTION

Plant conservation began in Madagascar prior to colonization in 1895, when the King Andrianampoinimerina banned cutting down trees in natural forests without a written logging permit (Henkel 2002, Tyson 2000). Although huge efforts have been made to achieve conservation, the management of forests and protected areas still needs improvement. Many environmental practitioners have realized that to maintain ecosystem services, managing sustainable forests and protected areas urgently need stakeholder participation (Worah 2008). Ecological services facilitate agriculture production; plants are used for medicine and as food, all of which are crucial for the survival of the Malagasy people (Ministry of Environment and Forests 2008, 2010a, Richardson 2010). Recently, 1091 useful species were under the Plant Resources of Tropical Africa project. Yet these resources are highly threatened by the alarming deforestation and loss of plant biodiversity due to different factors (e.g. the conversion of forests into farmlands and over logging; the rate of deforesta-

tion, which was 0.55% from 2000 to 2005; MEFT, USAID, CI 2009). To better protect Malagasy forest ecosystems, various groups (e.g. local communities, NGOs, universities and conservation institutions at national and international levels) are working together to improve biodiversity conservation and to create new protected areas. The process of identifying and delimiting these sites, as well as establishing management systems, has been done in a participatory way based on scientific information. Currently, areas of approximately 7.2 M hectares representing various Malagasy ecosystems have been protected. In this regard, many conservation targets with threatened plant species are now protected. This paper describes three main participatory approaches used by Conservation International (CI) Madagascar to improve plant conservation in the country: (a) identification of Key Biodiversity Areas for plants (KBAs); (b) knowledge management at the global and national levels; and (c) creation of new protected areas. The term 'participatory' as used here means involving stakeholders in various steps of the life cycle of a given program, defining a vision, goals, and objec-

tives, participating in project implementation, and monitoring and sharing benefits (Qiaolun 2004, Tikare et al. 2001).

METHODS

Identification of Key Biodiversity Areas for plant species

Defining KBAs is a useful tool for conservation planning. The method that we use for the identification of plant KBAs is based on the criteria used by Birdlife International for Important Bird Areas (Eken et al. 2004), which are in turn based on the framework of irreplaceability and vulnerability widely used in systematic conservation planning (Margules & Pressey 2000). They include: (1) globally threatened species; (2) restricted-range species; (3) congregations of species that concentrate at particular sites during some stage of their life cycle; and (4) biome-restricted species assemblages (Eken et al. 2004). One criterion concerns vulnerability (the presence of globally threatened species), while the three others are related to various elements of irreplaceability.

Datasets used to identify Madagascar's KBAs for plants are: (a) the 2008 IUCN Red List of 282 threatened plant species (IUCN 2008); (b) data from some scientific sources such as the Assessment of Priority Areas for Plant Conservation (APAPC), project carried out by the Missouri Botanical Garden (MBG) in 2004 (Andriambololonera et al. 2004); and (c) data from universities and other research institutions. In addition, we identified Alliance for Zero Extinction (AZE) sites based on the following criteria:

- (1) Endangerment: An AZE site must contain at least one Endangered (EN) or Critically Endangered (CR) species, as listed in the IUCN Red List.
- (2) Irreplaceability: An AZE site should only be designated if it is the sole area where an EN or CR species occurs, or contains the overwhelming proportion of the known resident population of the EN or CR species for at least one life history segment.
- (3) Discreteness: The area must have a definable boundary within which the character of habitats, biological communities, and/or management issues have more in common with each other than they do with those in adjacent areas (www.zeroextinction.org). AZE sites contain the last remaining populations of critically Endangered or Endangered species (Ricketts et al. 2006).

Based on these datasets, we analyzed the distribution areas of IUCN Red List plant species (IUCN 2008) and mapped them with the partners' participation to obtain Plant KBAs.

Knowledge management at the global and national levels

Our goal is to improve scientific knowledge on threatened plant species. National and international universities, research institutions, conservation NGOs, and other stakeholders are working together to enhance conservation efforts. Then CI provides technical and financial support to its partners to improve scientific knowledge management on threatened plant species and to publish this information. Based on the KBAs and IUCN Red List species, biological research has been prioritized annually to improve knowledge on threatened species. Research in areas such as population

dynamics, ecology, and forest restoration; have been conducted in collaboration with our partners. CI contributes to global species assessments in collaboration with IUCN experts and the Madagascar Plant Specialist Group. Various activities such as supporting research to feed biodiversity databases (e.g. the World Biodiversity Database and other plant database) and communicating data to our partners (e.g. the ONE – 'Office National pour l'Environnement', the National Environment Office – which manages the Clearing House Mechanism and the Convention on Biological Diversity, hereafter CBD) have been established. These datasets are useful for the establishment of the National CBD report and the Environmental Status National report, for the process of establishing protected areas, and for the success of conservation action.

Protected Areas Establishment

The vision of tripling protected areas in Madagascar from 1.7 million hectares to six million hectares, corresponding to 10% of the country's total area (Rasoavahiny et al. 2008), has been implemented since 2003. This effort contributes to the achievement of the 2010 national biodiversity targets 1 (at least 10% of each of the world's ecological regions effectively protected) and 2 (areas of particular importance to biodiversity protected) (Ministry of Environment and Forests 2010a).

The goal of our effort is to identify priority areas that maximize biodiversity conservation over six million ha based on the analysis of the number of species within existing protected areas and species and particular habitats that should be protected.

The objectives of the Madagascar Protected Areas System (known by its acronym in French, SAPM) are: (a) to conserve the full array of the unique biodiversity of Madagascar (ecosystems, species and genetic variability); (b) to conserve the Malagasy cultural heritage associated with biodiversity; and (c) to maintain and foster wise uses of natural resources in order to contribute to poverty alleviation and sustainable development.

To help increase the area protected in Madagascar, CI provides technical and financial support for data collection and analysis for conservation planning, establishes useful tools related to this process, and implements the protected area management process in the field, in order to help achieve the fundamental goals of the SAPM.

The fundamental principles on which the SAPM process is based are as follows: (a) use scientific approaches for the planning and management of protected areas, (b) engage all stakeholder sectors and all partners during consultation and dialogue; (c) involve the local community in protected areas management; (d) implement principles of good governance, and e) ensure that local communities are the first beneficiaries in the implementation of the SAPM initiative. Various processes, such as site identification, delimitation, and management are carried out in a participative way based on scientific information. Conservation International contributes directly to the implementation of these principles within its two main target sites: the Fandriana-Vondrozo Corridor and



Figure 1 – Map of New Protected Areas Network. Ministry of Environment and Forests, 2009.

Ankeniheny Zahamena Corridor, while collaborating with its partners to support other protected areas.

RESULTS

Identification of Key Biodiversity Areas for plants

Based on 537 threatened species (IUCN 2008) from eight taxonomic groups (Amphibians, Birds, Gastropods, Shrimps, Freshwater fish, Mammals, Plants, Reptiles), Conservation International Madagascar has identified 160 Key Biodiversi-

ty Areas (Rakotobe et al. 2005), 89 of which are home to 238 threatened plant species. The distribution of the 238 remaining threatened species needs to be studied (electronic appendix). Considering the high total level plant species diversity in Madagascar (estimated at 12,000 to 14,000 species; Key Biodiversity Areas for plants: Guillaumet & Koechlin 1971, Phillipson et al. 2006, Goodman 2008, Ramananjahary & Andriambololonera 2010), it is clear that significant additional effort is needed to assess the conservation status of Malagasy plant species.

Knowledge management at local, national and global levels

Although Madagascar has a remarkably diverse flora, the management of information about plants at the global, national and local levels is still very limited, but improving. As of 2007, 700 plant species had been assessed based on the IUCN Red List criteria (Ministry of Environment and Forests 2010a); by 2009, about 1850 species had been assessed and submitted to the IUCN for inclusion on the Red List, including 504 species classified as Critically Endangered species, 868 as Endangered species, and 476 as Vulnerable (Ministry of Environment and Forests 2010a). The significant portion of the available scientific data is captured into existing database [e.g. the World Biodiversity Database (WDBD) for threatened species, the Clearing House Mechanism (CHM/CDB) managed by the National Office for Environment (ONE), the GSPM database of the Madagascar Plant Specialist Group, and the TROPICOS database maintained by MBG]. Various important publications (e.g. the Atlas of Madagascar Vegetation, the Species Guide of Madagascar's endemic plant families) have resulted from these collaborative partnerships.

Protected Areas Creation in Madagascar

About 2,113,333 ha are currently protected in Madagascar within 44 protected areas under IUCN categories I (Strict Nature Reserves), II (National Parks), and IV (Habitat/ Species Management Areas), all managed by the Madagascar National Parks. A total of 95 new protected areas covering about 4,717,751 ha have been created, most of which fall are under categories V (Protected Landscape and Seascape) and VI (Managed Resource Protected Areas). Furthermore, a total of 7.2M additional ha are about to be protected (Ministry of Environment and Forests 2010b). Conservation International contributes to technical and financial supports for 38 of these new protected areas (encompassing an area of about 3 million hectares) (fig. 1).

CONCLUSION

The participatory approach is one of the best ways to improve the management of protected areas and knowledge, and the conservation of biodiversity. Local communities and environmental practitioners from different organizations, NGOs, and national and international institutions collaborate together to collect biodiversity data and protect habitats. Conservation International and its partners work within 38 of Madagascar's 114 new protected areas, where over 250 threatened species and about 2700 endemic plant species in 237 families are now being protected. These conservation efforts need to be amplified, and local people living near protected areas should be the first actors in the efforts to achieve lasting conservation outcomes.

SUPPLEMENTARY DATA

Supplementary material is available in pdf format at the Supplementary Data Site of publications from the National Botanic Garden of Belgium (<http://www.nbgpublisher.be> >

SBB50 > folder 563) and consists of a map of the Key Biodiversity Areas.

ACKNOWLEDGMENTS

We would like to express our sincere gratitude to Andriamaro Luciano, David Knox, Rabarison Harison, Rollande Finoana, Randrianasolo Harison for their collaboration in collecting, analyzing, and mapping data. Our great appreciation also goes to Pete Lowry, Jeannie Raharimampionona, Sylvain Razafimandimbison, and all reviewers for comments on an early version of this paper. We are very grateful to Conservation International, Madagascar Program for funding this research and Madagascar Plant Specialist Group (GSPM) for their collaboration in collecting data.

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- Manuscript received 27 Oct. 2010; accepted in revised version 29 Mar. 2012.
- Communicating Editor: Porter P. Lowry II.



Progrès du Projet Millennium Seed Bank à Madagascar

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The Millennium Seed Bank Project in Madagascar: progress made in seed collecting

Background – Madagascar is a country where the biodiversity has a high rate of endemism and also where the degradation of the biodiversity is one of the most alarming in the world. Many species of plant are endangered of extinction or have already disappeared. The Millennium Seed Bank Project (MSBP) is an *ex situ* conservation project which started at the end of the year 2000 in Madagascar. The objective of the project is to collect and preserve 10% of the flora of the arid and semi-arid zones which is approximately 1000 species over ten years. At the beginning of the project, the collecting trips were focused only in the Southern and South-western part of Madagascar. Later, the collecting sites were widened, more in north and on the high plateau of Madagascar. As the flora is badly known, phenology and the distribution are not known for the majority of the species and a high proportion of species have very restricted distributions, new strategies were adopted to improve the results.

Methods – The data analysis has been done by using the ArcView 3.3 and spatial Analyst software. The data used for all analysis are based on the collections done under the phase I of the project from 2000 to 2009. For each defined unit of area, ArcView calculates diversity based on the numbers allocated to each species with an adopted resolution of 0.5° which equals 55 × 55 km.

Key results – Approximately 1200 species of plants were collected in less than ten years.

Conclusions – Madagascar is the first country partner of the MSB Project to achieve its target. The six collecting zones in the arid and semi-arid regions were all visited. Nevertheless, much remains to be made especially to optimize the numbers of seeds sampled for each species, and also to prioritise the collect of Euphorbia and Orchids which are the most exploited for commercial purposes.

Key words – Arid and semi-arid zones, Madagascar, *ex situ* conservation, seed collecting.

Contexte – Madagascar est un pays où la biodiversité possède un taux d'endémisme élevé et aussi où la dégradation de la biodiversité est l'une des plus alarmantes au monde. A cause de ceci, plusieurs espèces de plante sont menacées de disparaître ou ont déjà disparu. Le projet Millennium Seed Bank (MSBP) est un projet de conservation *ex situ* qui a commencé à la fin de l'année 2000 à Madagascar. Le but du projet est de rassembler et de conserver 10% de la flore des zones arides et semi-arides, ce qui représente environ 1000 espèces à collecter en dix ans. Au début du projet, les collectes se sont focalisées seulement dans la partie Sud et Sud Ouest de Madagascar. Plus tard, les sites de collectes ont été élargis, plus au Nord sur les hauts plateaux malgaches.

Méthodes – Le logiciel ArcView 3.3 et Spatial Analyst ont été utilisés pour les analyses des données. La base de données utilisée a été celle des collections faites au cours de la phase I du projet, entre 2000 et 2009. Pour chaque unité de surface définie, ArcView calcule la diversité en se basant sur les numéros attribués à chaque espèce avec une résolution adoptée de 0,5° soit environ 55 × 55 km.

Résultats clés – Environ 1200 espèces de plantes ont été récoltées en moins de dix ans.

Conclusions – Madagascar est le premier pays partenaire du projet MSB à atteindre son objectif. Les six zones de récoltes dans les zones arides et semi-arides ont toutes été visitées. Néanmoins, beaucoup reste à faire surtout dans l'amélioration du nombre de graines récoltées pour chaque espèce, et dans la récolte des Euphorbes et Orchidées qui sont les plus exploitées commercialement.

INTRODUCTION

Philbert Commerson avait dit que Madagascar est la terre promise pour les naturalistes. Madagascar compte entre 10 000 et 14 000 espèces de plantes vasculaires (Ramananjahary et al. 2010) dont 90% sont endémiques. Le pays jouit d'un climat varié allant d'un climat sec, subhumide à un climat humide. La végétation diffère en fonction des conditions écologiques, allant d'une végétation sèche à une végétation humide luxuriante, d'une formation basse côtière à une végétation de haute altitude, d'une formation graminéenne à une forêt dense. D'un autre côté, Madagascar est un pays où règne la destruction massive et rapide de la couverture végétale. Chaque année, environ 200 000 ha de végétation partent en fumée. En outre, plusieurs espèces envahissantes pouvant nuire à la survie des espèces autochtones ont été introduites.

Le projet Millennium Seed Bank (MSBP) est un projet de conservation *ex situ* qui avait commencé à la fin de l'année 2000 à Madagascar. Le projet est basé à Wakehurst en Angleterre et travaille avec 127 partenaires dans environ cinquante pays dans le monde. A Madagascar, le projet travaille en collaboration avec le Silo National des Graines Forestières (SNGF). Son objectif sur dix ans, comme dans tous les pays partenaires, est de récolter et de conserver les graines de 10% de la flore des zones arides et semi-arides, soit environ mille

Tableau 1 – Liste des familles collectées les plus représentées en nombre d'espèces.

Familles	Nombre d'espèces
Fabaceae	210
Rubiaceae	83
Asteraceae	68
Euphorbiaceae	50
Tiliaceae	44
Convolvulaceae	36
Cyperaceae	36
Malvaceae	33
Sterculiaceae	33
Poaceae	29

espèces. A Madagascar, nous avons priorisé les espèces succulentes qui sont exploitées à des fins commerciales et les espèces rares et menacées. Ces graines seront conservées à long terme dans les deux banques de graines au SNGF et à Wakehurst en vue d'une restauration ou réintroduction des ces espèces dans leurs habitats naturels si un jour elles viennent à disparaître. Les collectes des graines sont faites dans les zones arides et semi-arides, là où les graines orthodoxes qui sont conservables à long terme abondent. Au début du projet, les collectes ont été concentrées seulement dans les zones sud et sud ouest de Madagascar. Plus tard, vers la fin de l'année 2003, les sites de récoltes ont été étendus pour couvrir toutes les zones arides et semi-arides à Madagascar.

MATERIELS ET METHODES

Nous nous sommes basés sur les collections d'espèces en fruit récoltées à Madagascar et répertoriées dans la base de données de Royal Botanic Gardens Kew à Madagascar. Nous avons fait recours aux logiciels ArcView 3.3 et spatial Analyst pour l'analyse des données. La carte des territoires phytogéographiques de Madagascar par Humbert (1955) et l'Atlas de la végétation de Madagascar (Moat & Smith 2007) sous forme de grilles de 0.0003°, soit une résolution de 30 × 30 m ont été utilisées comme fond de carte. La base de données MSBP est reliée à chaque couche sur ArcView. Ceci permet de créer une nouvelle base de données où chaque échantillon possède désormais une information sur les caractéristiques écologiques du site de récolte. Le tableau obtenu à partir d'ArcView est ensuite utilisé pour estimer la variation de la richesse spécifique le long d'un gradient écologique. Pour l'analyse à partir du logiciel spatial analyst, chaque nom d'espèces est codifié sous forme numérique pour pouvoir être analysé. Pour chaque unité de surface définie, ArcView calcule la diversité en se basant sur les numéros attribués à chaque espèce avec une résolution adoptée de 0,5° soit environ 55 × 55 km.

RESULTATS

Depuis le commencement du projet vers la fin de l'année 2000 jusqu'au début de l'année 2009, les zones de récoltes couvrent presque Madagascar à l'exception de la partie ori-

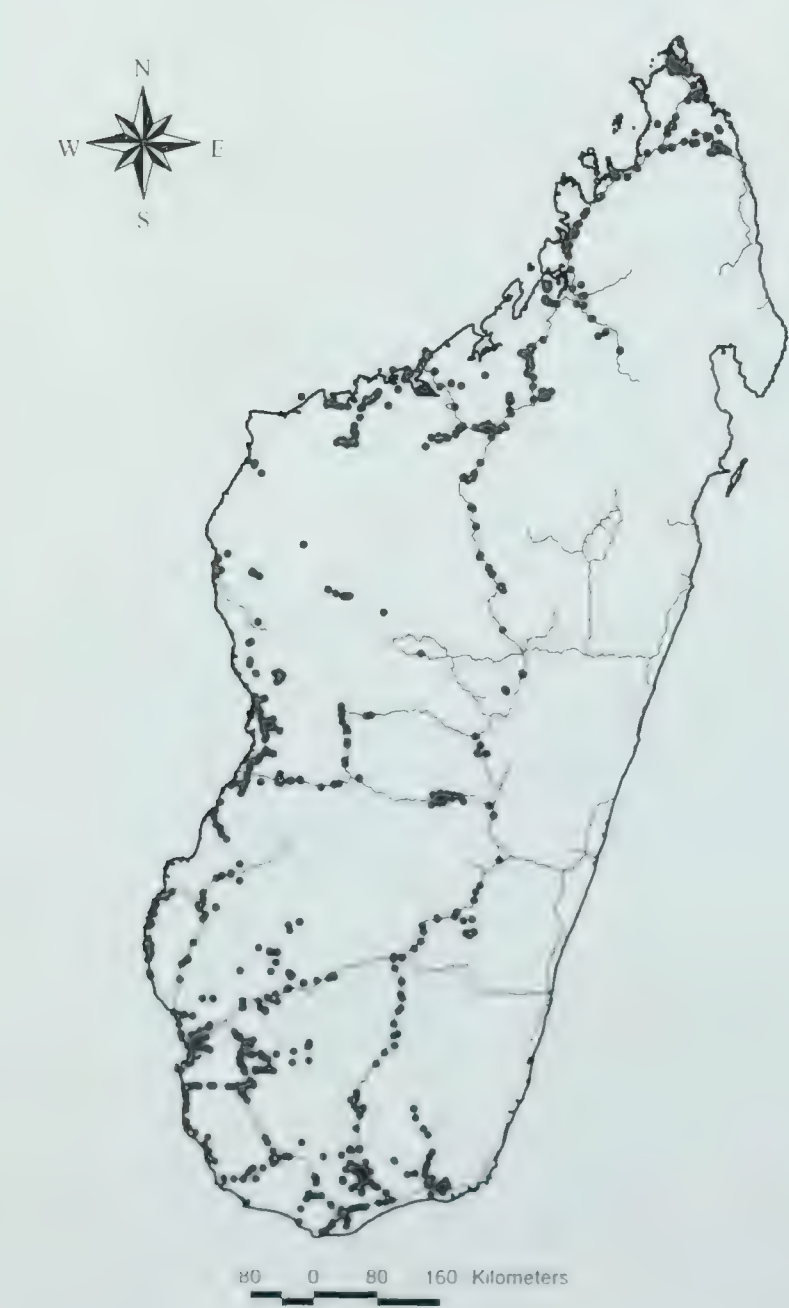


Figure 1 – Distribution de toutes les collections de 2000 à 2009.

Tableau 2 – Nombre des espèces récoltées en fonction des domaines phytogéographiques.

Domaines phytogéographiques	Nombre d'espèces
Ouest	735
Sud	365
Hauts plateaux centraux	142
Versants occidentaux des hauts plateaux	136
Hautes montagnes	13
Domaine de Sambirano	8

entale de l'île (fig. 1). Au niveau floristique, 1 987 collections ont été faites et sont réparties en 119 familles, 519 genres et environ 1 200 espèces. Le tableau 1 montre les dix familles les plus représentées en nombre d'espèces. Bon nombre de ces familles ont été également identifiées comme les plus représentées au niveau générique.

Parmi les domaines phytogéographiques, le domaine de l'Ouest a fait l'objet de la collecte la plus importante (avec 735 espèces) tandis que seulement huit espèces ont été collectées au de Sambirano (tableau 2).

Les résultats des analyses des sites en fonction des espèces récoltées montrent que le District de Betioky-Sud enregistre la plus haute valeur avec ses 109 espèces récoltées (tableau 3).

En termes de types de végétation, neuf sur les quatorze décrits dans l'Atlas de la végétation de Madagascar (Moat & Smith 2007) ont été visités par l'équipe de récolte (tableau 4). Cependant, presque la totalité des récoltes (94%) ont été faites seulement dans quatre types de végétation correspondants aux zones arides et subarides constituant les habitats potentiels des espèces à graines orthodoxes.

Parmi les espèces succulentes cibles, soixante ont été récoltées: 23 espèces du genre *Aloe*, six espèces du genre *Pachypodium*, 18 espèces du genre *Kalanchoe*, huit espèces du genre *Euphorbia* et cinq espèces de la famille des *Didieraceae*.

Pour les Aloes composés de 100% d'espèces endémiques, les espèces récoltées ne représentent que 15% seulement des espèces à Madagascar. En ce qui concerne le genre *Pachypodium*, six seulement sur les 18 espèces malgaches (Rapanarivo 1999) ont été collectées. Pour la famille des Or-

Tableau 3 – Nombre d'espèces récoltées en fonction des sites.

Sites	Nombre d'espèces
Betioky-Sud	109
Ambatofinandrahana	93
Toliary II	78
Ambovombe-Androy	74
Amboasary-Sud	68
Iharana (Vohémar)	58
Boriziny (Port-Bergé)	55
Antsirabe II	54
Sakaraha	46
Ambalavao	37

Tableau 4 – Pourcentage des espèces récoltées dans les différents types de végétation.

Type de végétation	% des espèces récoltées
Mosaïque formations herbeuses boisées-formations boisées de plateau	31,05
Mosaïque formations herbeuses boisées-formations buissonnantes	30,83
Forêt sèche de l'ouest	17,14
Forêt sèche épineuse du sud-ouest	15,08
Forêt sub-humide de l'ouest	3,09
Formation buissonnante côtière du sud-ouest	1,40
Forêt humide dégradée	0,88
Forêt de Tapia	0,29
Forêt humide de l'ouest	0,22

chidaceae qui compte à peu près 1 000 espèces dont 85% sont endémiques (Hermans et al. 2007), 28 seulement sont actuellement représentées dans les collections.

Pour les espèces charismatiques de la famille des *Didieraceae* qui caractérise la végétation du sud et du sud ouest de Madagascar, cinq sur les onze espèces ont été récoltées.

Enfin, le tableau 5 montre la liste des vingt sites les plus importants pour le nombre moyen d'espèces récoltées, offrant une autre vision des résultats présentés dans le tableau 3.

DISCUSSION

Le nombre élevé d'espèces récoltés dans les domaines phytogéographiques de l'Ouest et du Sud (tableau 2) peut s'expliquer du fait que ces zones se trouvent là où règne un climat sec et subaride. Les formations végétales sont alors riches en espèces de plantes à graines orthodoxes. Par conséquent, la plupart des missions de terrain se sont orientées vers ces zones. En revanche, pour les domaines de hautes montagnes, bien que ces zones soient riches en espèces de plantes à graines orthodoxes telles que les graminées et *Helichrysum*, elles restent encore peu explorées par l'équipe de récolte. Ceci explique la faible valeur de nombre des espèces récoltées dans ces zones.

Dans la plupart des ouvrages sur la diversité floristique malgache, quatre grandes familles de plantes se démarquent par leur nombre élevé d'espèces, à savoir: *Euphorbiaceae*, *Fabaceae*, *Rubiaceae* et *Poaceae* (Repoblikan'i Madagaskara 1997). Notre liste présentée sur le tableau 1 en rend bien compte, car on y retrouve ces quatre familles, même si la famille de *Poaceae* se trouve à la dixième place. Ceci est principalement dû au fait que notre équipe a seulement commencé à récolter les espèces de graminées tardivement. Par ailleurs, même si la famille des *Orchidaceae* constitue une grande famille à Madagascar, elle ne figure pas dans la liste des familles les plus riches en espèces récoltées, car nos collectes se sont faites dans les zones arides et semi-arides, là où les espèces d'orchidées sont rares. En ce qui concerne les espèces succulentes cibles, huit espèces seulement ont été

Tableau 5 – Nombre moyen d’espèces récoltées en fonction des sites.

Sites	Nombre moyen d’espèces récoltées
Ambatofinandrahana	5,71
Vohimarina (Iharana)	5,31
Morondava	4,89
Ambalavao	4,88
Antsirabe II	4,82
Belon-i Tsiribihina	4,54
Antsiranana II	4,5
Mahajanga II	4,18
Morombe	3,87
Analalava	3,86
Boriziny (Port-Berg.)	3,73
Betioky-Sud	3,67
Sakaraha	3,63
Mampikony	3,54
Ambato-Boina	3,42
Toliary II	3,37
Ambovombe-Androy	3,24
Ampanihy	3,18
Ihosy	2,81
Amboasary-Sud	2,35

récoltées pour le genre *Euphorbia* jusqu’à maintenant, bien que le genre constitue une des composantes essentielles des fourrés secs dans le sud et sud ouest malgache. Nos analyses enregistrent 35 espèces du genre dans les formations sèches du sud et du sud-ouest. Ceci s’explique par le fait qu’il est difficile de récolter le nombre minimum de graines (500) d’une espèce du genre *Euphorbia* pour assurer une conservation optimale. Une solution devrait être adoptée pour améliorer le nombre d’espèces conservé dans les banques de graines.

CONCLUSION

A ce jour, Madagascar est le premier pays partenaire du projet MSB à atteindre son objectif, grâce aux efforts déployés aux niveaux matériels et techniques. Les six zones de récoltes ont pu être visitées pendant cette première phase du projet. Par conséquent, la grande majorité des flores des zones sèches et semi-arides malgaches sont représentées dans les collections.

Néanmoins, beaucoup reste à faire à Madagascar pour la prochaine phase du projet. En effet, la liste des espèces cibles devrait être revue. Nos constatations durant les multi-

ples missions de terrain montrent que les plantes grasses sont plus exposées aux récoltes illicites à des fins commerciales, à la destruction des habitats comme dans le cas des Aloaceae, Apocynaceae (*Pachypodium*), Orchidaceae et Euphorbiaceae, ou à l’exploitation des parties ligneuses pour la construction (cas des Didieraceae)

Des efforts doivent être donc déployés pour collecter d’autres espèces de plantes grasses qui n’ont pas encore récoltées jusqu’ici, surtout pour les espèces d’*Euphorbia*. Pour ces espèces les collectes devraient se faire en plusieurs étapes pour atteindre un nombre minimum de graines.

REMERCIEMENTS

Nous adressons nos vifs remerciements à tous les personnels du Royal Botanic Gardens Kew à Madagascar et du Silo National des Graines Forestières qui ont participé à la réalisation de ce projet, le Missouri Botanical Garden qui nous a fourni ses données pour la programmation des missions de terrain, le Pr Lolona Ramamonjisoa qui avait eu l’amabilité de consacrer ses précieux temps pour examiner ce document, le Dr Mijoro Rakotoarinivo qui a beaucoup contribué à l’analyse des données, Mr Stuart Cable qui nous a soutenu techniquement, Mr Guillaume Besnard qui a revu la version finale de ce manuscrit et le Dr Moctar Sacandé, Responsable du projet Millennium Seed Bank à Madagascar.

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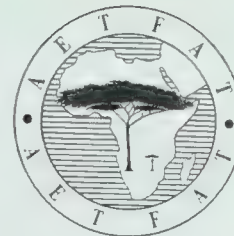
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Manuscript received 23 Sep. 2010; accepted in revised version 15 Sep. 2011.

Communicating Editor: Sylvain Razafimandimbison.



Dynamique spatiale et diversité floristique de la Réserve de Faune de Togodo au Sud Est du Togo (Afrique de l'Ouest)

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Spatial dynamic and floristic diversity of Togodo Fauna Reserve in the South of Togo (West Africa)

Background – The Togodo Fauna Reserve presents a great ecological interest because of its semi-deciduous forest relics. This Reserve represents forest ecosystems of the Dahomey Gap ecoregion.

Methods – The Reserve's spatial dynamic was investigated, using aerial photos (1949 and 1979) and a satellite image (1998). For the three reference years, areas of different types of vegetation and number of forest patches were determined in order to analyse forest cover change during the last fifty years. Floristic diversity of each vegetation unit was assessed through determination of diversity indices (Shannon index, equitability) and the status of 'key' species was determined based on calculation of rarity index.

Key results – Analysis of forest cover change indicated a general trend of areas covered with vegetation decrease from 8,094 ha in 1949 to 4,479 ha in 1998. These forest patches are more and more split, this lead to forest decline with a rate estimated at 56 ha/year between 1949 and 1979 and 101 ha/year between 1979 and 1998. In total, 485 plant species have been recorded during the botanical investigation conducted in the Reserve. The particular interest of the forest patches in biological diversity preservation is expressed by the 'exclusive key species' presence in this protected area for which rarity indexes were found to be often very high such as for *Balanites wilsoniana*, *Schrebera arborea* and *Strychnos usambarensis*. These species are also considered as endangered species because Togodo forests represented the last refuges in Togo. Eighteen taxa are newly recorded for the flora of Togo.

Key words – Forest decline, biodiversity sanctuaries, exclusive species, Togodo Fauna Reserve, Togo.

Contexte – La Réserve de Faune de Togodo présente un grand intérêt écologique à cause de la présence des vestiges de forêts semi-décidues. Cette Réserve est très représentative des écosystèmes forestiers de l'écorégion du Couloir du Dahomey.

Méthodes – L'étude de la dynamique spatiale de la Réserve s'est appuyée sur des photographies aériennes (de 1949 et de 1979) et sur une image satellitaire (de 1998). Pour les trois années de référence, les superficies des types de végétation et le nombre de fragments forestiers sont déterminés et permettent d'analyser l'évolution de la végétation au cours des cinquante dernières années. La diversité floristique de chaque unité de végétation est évaluée à travers le calcul des indices de diversité (indice de Shannon, équitabilité) et le statut des 'espèces clés' est précisé au moyen du calcul de leur indice de raréfaction.

Résultats-clés – L'analyse de l'évolution de la végétation indique une tendance générale à la régression des surfaces forestières passant de 8 094 ha en 1949 à 4 479 ha en 1998. Ces îlots forestiers se fragmentent de plus en plus entraînant leur disparition avec un rythme estimé à 56 ha/an entre 1949 et 1979 et à 101 ha/an entre 1979 et 1998. Au total, 485 espèces végétales ont été recensées à la suite des prospections botaniques conduites dans la Réserve. L'intérêt particulier des fragments de forêt dans la conservation de la diversité biologique se traduit par l'existence dans cette aire protégée 'd'espèces clés exclusives' dont les indices de rareté sont pour la plupart très élevés telles que *Balanites wilsoniana*, *Schrebera arborea* et *Strychnos usambarensis*. Elles sont également considérées comme des espèces en danger critique car les forêts de Togodo constituent leurs derniers refuges au Togo. Dix huit taxons sont nouvellement signalés pour la flore du Togo.

INTRODUCTION

En Afrique tropicale, les puissances coloniales avaient posé d'importants actes en matière de gestion durable des ressources naturelles à travers la réglementation de l'usage traditionnel et la délimitation des aires protégées (MacKinnon & MacKinnon 1986). Le souci majeur qui animait la création de ces domaines était la conservation d'une part importante de la diversité des pays concernés (Shackleton 2000) car les aires protégées sont considérées comme les pierres angulaires des stratégies de conservation à travers le monde (Clerici et al. 2007). C'est ainsi qu'au Togo, entre 1939 et 1955, environ 801 443 ha soit 14,2% du territoire (56 600 km²) ont été protégés. Parmi les aires protégées créées, la Réserve de faune de Togodo (RFT) présente un grand intérêt écologique pour le Togo à cause de son importante biodiversité. C'est dans cette Réserve que se trouvent les plus importants vestiges de forêt (environ 4500 ha) dans le paysage dénudé et fortement anthropisé de la plaine côtière du Sud Togo (Kokou & Caballé 2000). Cette Réserve est la seule aire protégée située dans la zone guinéenne du pays et constitue l'un des quatre sites que le pays a actuellement inscrit sur la liste des zones humides d'importance internationale (sites RAMSAR). Elle renferme les derniers troupeaux de buffles du Togo après que la faune sauvage ait été sauvagement décimée lors des troubles sociopolitiques que le pays a traversés entre 1990 et 1993. Elle abrite le Singe à ventre rouge (*Cercopithecus erythrogaster*), espèce vulnérable et menacée, endémique au Sud du Togo et au Bénin (Houngbedji 2010). Sur le plan touristique, elle est assez proche des grandes villes côtières, ce qui la rend facile d'accès par rapport aux parcs nationaux togolais qui sont dans les zones soudaniennes septentrionales.

La RFT est très représentative des écosystèmes reliques de l'écorégion du Couloir du Dahomey (Jenik 1994). Dans ce couloir, la savane descend jusqu'à la côte (White 1986, Jenik 1994, Salzmann & Hoelzmann 2005). De ce fait, les îlots de forêt de la Réserve constituent alors l'un des rares écosystèmes forestiers du Togo. Il s'agit des forêts de type guinéen, qui font la transition entre la forêt semi-caducifoliée et la forêt sèche. Kokou et al. (2008) affirment qu'il s'agit de 'dry semi-deciduous forest' au sens de Hall & Swaine (1981). Adomou (2005) signale qu'il s'agit de forêts semi-caducifoliées à *Triplochiton scleroxylon*-*Celtis zenkeri* qui auraient occupées le sud du Togo et du Bénin jusqu'à la limite actuelle des savanes guinéo-soudaniennes (Salzmann & Hoelzmann 2005).

Mais depuis sa création, à l'instar de l'ensemble des aires protégées du pays, elle a fait l'objet d'une gestion unilatérale et de façon répressive par l'Etat, aliénant ainsi les droits des communautés locales. Cette politique de conservation et de protection a fini par soulever l'hostilité des populations, surtout celles riveraines de ces domaines protégés et ce d'autant plus que ces populations commençaient à souffrir de l'insuffisance de terres cultivables suite à la croissance démographique des trente dernières années. Mais ces dernières années, l'Etat réfléchit sur les nouvelles stratégies de gestion durable à adopter pour l'ensemble des domaines protégés du pays. De ce fait, il est important de connaître la situation actuelle des ressources biologiques dans la RFT, le sens de l'évolution de la végétation et tout particulièrement des îlots forestiers qui

font d'elle une aire protégée unique dans l'écorégion. C'est dans cette perspective que cette étude est réalisée pour établir un diagnostic sur la dynamique forestière depuis 1949, l'état de la conservation des formations végétales et la diversité floristique afférente. Il s'agit d'identifier les habitats reliques que sont les îlots de forêt, d'étudier l'évolution de leur surface au cours de cinquante dernières années, le degré de fragmentation et le risque d'extinction des 'espèces clés'. Les résultats vont aider à la prise de décision en ce qui concerne une gestion plus efficiente de cette aire protégée prioritaire du Togo.

MATERIELS ET METHODES

Description de la zone d'étude

La RFT est située entre 6°23' et 7° de latitude Nord et entre 1°23' et 1°34' de longitude Est (fig. 1) et couvre actuellement une superficie totale de 25 500 ha. Elle est composée de deux entités, à savoir la forêt classée de Togodo Sud (15 000 ha, classée par arrêté n° 534/EF du 4 Juil. 1954) et la forêt classée de Togodo Nord (10 500 ha, classée par l'arrêté n° 174/EF du 26 Fév. 1954). D'après l'arrêté n° 003 MERF/CAB du 3 Mai 2005, la forêt classée de Togodo Sud va être érigée en Parc National et se verra attribuer des fonctions de (i) protéger les forêts reliques de l'aire protégée à des fins spirituelles, scientifiques, éducatives, récréatives et touristiques, (ii) perpétuer, dans les conditions naturelles, les éléments écologiques, géomorphologiques, sacrés et esthétiques et (iii) garantir une stabilité et une diversité économique locale. Quant à la partie nord de la Réserve, elle est requalifiée en zone de gestion des ressources naturelles par l'arrêté n° 005 MERF/CAB du 2 Fév. 2005.

L'ensemble de ce secteur se présente sous forme d'une large plaine mollement ondulée dont l'altitude varie de 10 à 50 m. Le seul relief notable est une colline (le mont Gbéto) qui culmine à 228 m. Des affleurements de migmatites apparaissent en certains endroits notamment vers le nord de la Réserve. Sur le reste de l'aire protégée, se trouvent des gneiss et des micaschistes dont la décomposition donne des sols argileux avec un horizon de surface sableux. Le réseau hydrographique fait partie dans son ensemble du bassin sédimentaire du Mono. Ses affluents de la rive droite traversent le périmètre de la Réserve ou y prennent leur source.

Le climat est subéquatorial, avec une grande saison des pluies de Mars à Juillet et une petite saison des pluies de Septembre à Novembre. Ces deux saisons de pluies sont entrecoupées par une grande saison sèche et une petite saison sèche. Dans la classification de Köppen, le climat est de type AW avec 3 à 5 mois écologiquement secs (Demangeot 1999). La moyenne annuelle des précipitations est de 1 000 à 1 200 mm et la température moyenne annuelle est voisine de 27°C.

Analyse diachronique du couvert végétal dans la RFT et sa zone périphérique

L'étude de la dynamique spatiale de la Réserve et de sa zone périphérique s'appuie essentiellement sur l'interprétation des photographies aériennes et d'une image satellite. Les photographies aériennes utilisées sont celles de 1949 (1/50 000^e) et

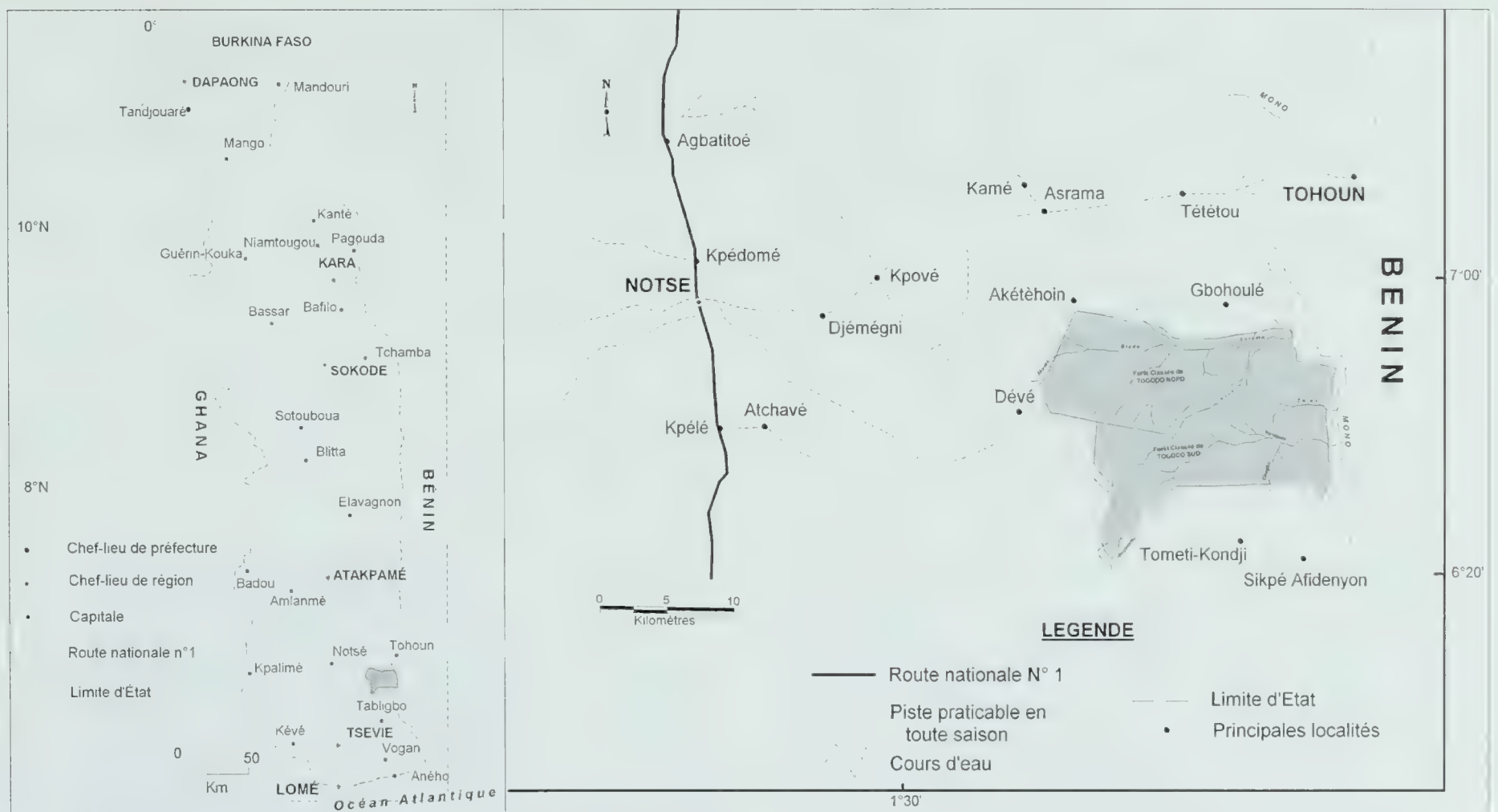


Figure 1 – Localisation de la Réserve de faune de Togodo.

de 1979 (1/30 000^e). L'état de l'évolution de la végétation en 1998 est obtenu à partir d'une image satellite SPOT XS 1B n°063-336 prise juste après les feux de brousse. Les cartes d'occupation du sol établies à partir des photographies aériennes (1949 et 1979) et de l'image satellitaire de 1998 ont servi de base pour la cartographie de la végétation et l'étude de ses modifications au cours des années 1949, 1979 et 1998.

A partir des photographies aériennes de 1949 et de 1979, les surfaces occupées par les forêts, les savanes, les jachères et les cultures ont été délimitées sur transparents. Celles-ci ont été numérisées et intégrées dans un Système d'Information Géographique (SIG), en utilisant le logiciel MapInfo v.7.5. Ceci a permis d'obtenir une carte d'occupation des sols à la même échelle pour les deux époques. Quant à l'image satellitaire de 1998, elle a constitué directement un support numérisé sous Géoconcept après géoréférencement à partir des coordonnées géographiques relevées à l'aide du GPS sur le terrain. Une carte de végétation est ainsi réalisée à partir de cette image où l'occupation des sols est plus détaillée que précédemment. Une phase de reconnaissance de terrain a été nécessaire afin de caractériser correctement les unités d'occupation du sol.

Les supports numériques obtenus à partir des deux photographies aériennes et de l'image satellite ont permis de calculer les superficies de chaque formation végétale et de déterminer le nombre de fragments forestiers sur chaque support. Ensuite, la démarche adoptée pour l'analyse diachronique a consisté à rattacher chaque unité de végétation déterminée sur les supports des photographies aériennes à une apparence ou un ensemble d'apparences qu'elle revêt sur l'image satellite. Une fois cette classification faite et le nombre de fragments forestiers et leur superficie respective déterminée, il est pos-

sible de calculer l'évolution de chacune des unités de végétation à travers les trois âges retenus par la formule ci-dessous:

$$Evolution (\%) = \frac{Surface_{annee1} - Surface_{annee2}}{Surface_{annee1}} \times 100$$

Inventaires floristiques

La méthode de collecte de données utilisée pour l'étude de la diversité floristique de la Réserve est celle des inventaires floristiques à travers les relevés sur des placettes rectangulaires de 500 m² (50 m × 10 m). Les placettes sont disposées en continu le long de transects d'une longueur de 500 m à 2 km. L'emplacement de ces transects était déterminé au préalable sur la carte d'occupation du sol de la Réserve selon l'accessibilité et la représentativité de chaque formation végétale. Au total, 182 placettes ont été échantillonnées, soit une superficie de 9,1 ha, représentant un taux de sondage de 0,4%.

Dans chaque parcelle, la liste des Angiospermes (arbres, arbustes, herbacées) a été réalisée (présence/absence). Les espèces non identifiées sur le terrain ont été récoltées et déterminées dans l'herbier de l'Université de Lomé (UL) au Togo. Les flores utilisées pour la détermination des espèces sont celles de Hutchinson & Dalziel (1954–1972), d'Aubréville (1959) et de Brunel et al. (1984). Lors des relevés floristiques, une fiche de descripteurs écologiques concernant le site de relevé a été renseignée simultanément sur le terrain. Ces descripteurs sont relatifs au type de végétation, à la géomorphologie, à la texture du sol et aux activités humaines (impact de feu, pâturage, coupe de bois).

Analyse de la diversité floristique

L'ensemble des relevés floristiques a été analysé par une Analyse Factorielle des Correspondances (Benzécri & Benzécri 1980) afin de préciser la distribution des espèces dans l'aire protégée. Il s'agit d'isoler et de caractériser les différents types de végétation présents dans la RFT.

La diversité floristique des différentes unités de végétations identifiées a été évaluée à travers des indices de diversité floristique (Hill 1973, Daget 1980). Ces indices ont été calculés sur les relevés de chacun des écosystèmes qui caractérisent la RFT (diversité- α). La signification des différences pour chaque indice a été testée par ANOVA (Test de Fisher) grâce au programme Minitab. La richesse floristique (N_0), représente le nombre total d'espèces; l'indice de Shannon est exprimé par la formule

$$I_{SH} = \sum_{i=1}^n p_i \log(p_i)$$

(n = le nombre d'espèces rencontrées et p_i = la probabilité qu'une espèce i soit présente dans un relevé).

En pratique, $p_i = q_i/Q$ où q_i est le nombre de relevés où l'espèce i a été observée et $Q = \sum_{i=1}^n q_i$.

Enfin l'équitabilité

$$(E_i = \frac{I_{SH}}{\log_2 N_0})$$

correspond au rapport entre la diversité observée et la diversité maximale possible étant donné le nombre d'espèces N_0 .

En outre le statut des espèces «clés» a été précisé en ce qui concerne particulièrement les espèces rares, exclusives c'est-à-dire des espèces inféodées seulement aux îlots forestiers de cette région du Togo, et nouvelles à la flore du Togo (Brunel et al. 1984, Akpagana 1992, Akpagana & Guelly 1994). Pour ce faire, un indice de raréfaction des espèces (Rarity-weighted Richness Index) a été calculé suivant l'équation de Géhu & Géhu (1980):

$$RI = \left[1 - \left(\frac{n_i}{N} \right) \right] \times 100$$

(avec RI = indice de raréfaction, n_i = nombre de relevés dans lequel l'espèce i est présente et N = nombre total de relevé). Conformément à cette relation, les espèces dont les RI < 80% sont considérées comme des espèces préférentielles, très fréquentes dans les forêts étudiées. Celles dont les RI > 80% sont rares. Dans une étude récente au Bénin, qui se trouve dans la même situation phytogéographique que le Togo, ce seuil de 80% a été retenu par Adomou (2005).

RESULTATS

Evolution de la végétation au cours des cinquante dernières années: la fragmentation forestière

L'examen des cartes de la RFT et sa zone périphérique fournit des renseignements importants sur l'évolution de la superficie forestière à cinquante années d'intervalle (1949 à 1998). La couverture de 1949 a révélé des complexes forestiers intacts notamment dans la partie septentrionale et méridionale,

aussi bien à l'intérieur qu'à l'extérieur de la Réserve. Il existait autour des villages de Gbohoulé, d'Akétèhoin et de Tométi-kondji d'importants massifs forestiers. Les limites entre forêts et savanes étaient nettes (fig. 2A). La surface totale de l'ensemble de ces massifs forestiers est estimée à 8 094 ha réparties en 79 fragments forestiers qui occupent chacun en moyenne 102 ha. Il n'existait qu'une seule tache de culture visible sur la photographie aérienne et dont la surface est estimée à 3 ha (tableau 1).

Entre 1949 et 1979, la forêt a régressé partout et plus fragmentée dans la RFT et sa zone périphérique. Les massifs forestiers autour des villages ont quasiment disparu. Ainsi, en 1979, la surface forestière de la Réserve est évaluée à 6 412 ha et on y dénombre 145 fragments forestiers dont la

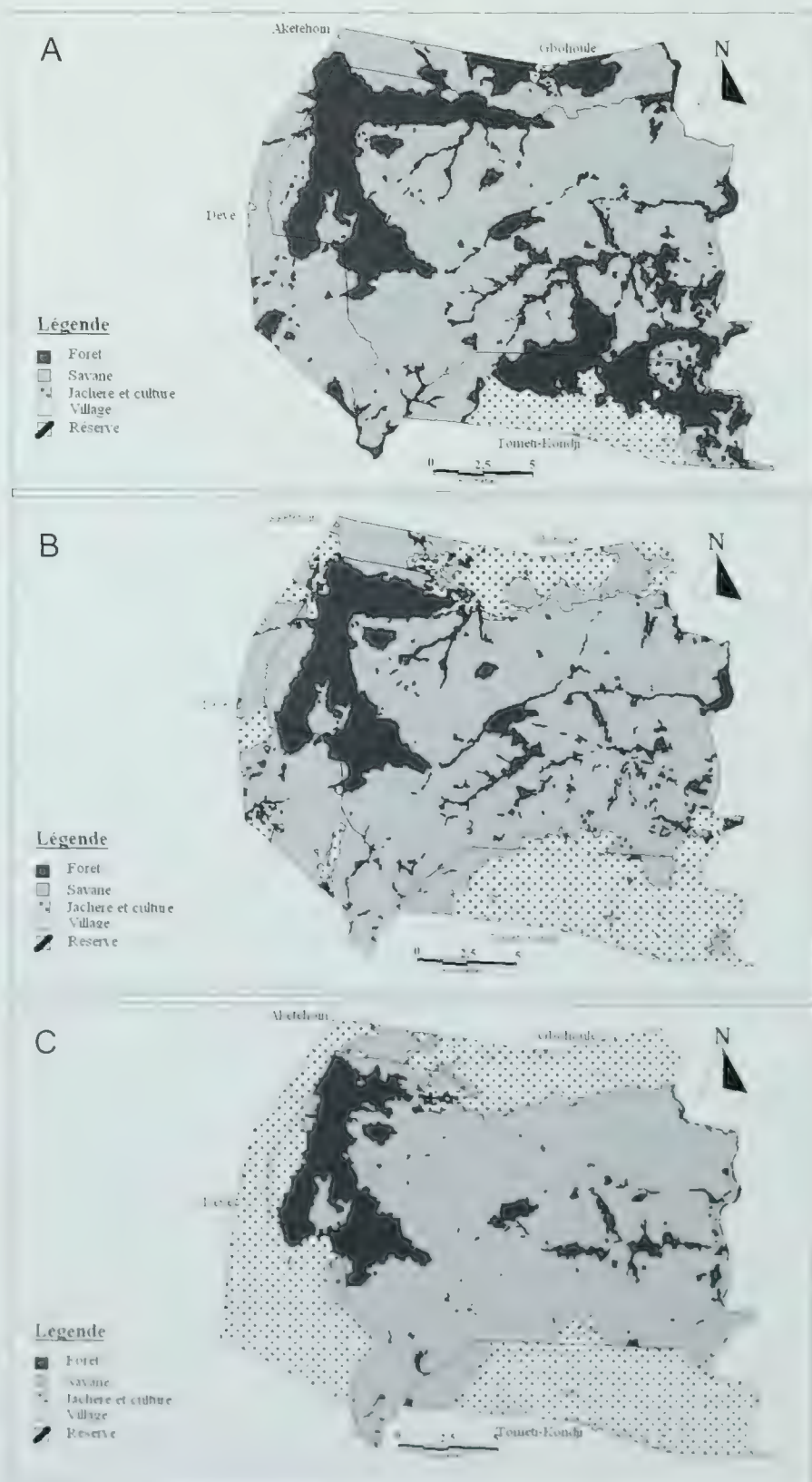


Figure 2 – Evolution du couvert végétal dans la RFT et sa zone périphérique: A, couverture de 1949; B, couverture de 1979; C, couverture de 1998. A & B, basées sur photographies aériennes; C, basée sur image satellitaire.

Tableau 1 – Indicateurs de fragmentation de la forêt dans la réserve de faune de Togodo.

Type de formation	1949	1979	1998
Fragments de forêt (effectif)	79	145	97
Surface moyenne des fragments de forêt (ha)	102	44	46
Surface totale des forêts (ha)	8 094	6 412	4 479
Tache de culture (effectif)	1	25	5
Surface totale de culture (ha)	3	1 315	635

surface moyenne de chaque est évalué à 44 ha. La proportion de superficie boisée transformée en champs et jachères est nettement plus forte dans les zones limitrophes de la Réserve. Le nombre de taches qui correspondent aux zones de cultures est égal à 25 et couvre une superficie totale évaluée à 1 315 ha (tableau 1). Un fort défrichement opéré dans la zone de Tométi-Kondji (zone 3) a éliminé quasiment toutes les formations forestières existantes sur ce terroir (fig. 2B). Le front de défrichement a progressé vers le nord au détriment de la forêt et a dépassé la limite sud de la RFT.

La situation au niveau du terroir de Gbohoulé (zone 1) est semblable. En 1979, il restait environ 20% de formation forestière initiale au milieu de laquelle s’est installé le village. A l’intérieur de la réserve, près de 21% de la superficie forestière a été reconvertie en espace agricole (fig. 2B). Il ne reste plus que de grands pieds de Ceiba pentandra dominant des surfaces mises en cultures. La dégradation des ressources forestières au niveau du terroir de Dédé (zone 2) a commencé plus tardivement à partir de 1979 (fig. 2B). Cette zone étant essentiellement constituée de savanes, l’effet des feux de brousse trop intenses a également entraîné une régression des stades forestiers.

De 1979 à 1998, l’encerclement de la RFT par les zones de cultures a été total (fig. 2C). En règle générale, les trois fronts de défrichement ne dépassent pas les limites de la Réserve, mais quelques percées sont cependant observées, notamment au Sud et à l’Est (fig. 2C). Ces défrichements ont été faits au détriment des savanes, les zones forestières ayant quasiment toutes disparu durant la période précédente. La dégradation de la partie septentrionale de l’îlot forestier principal de la Réserve s’est accentuée. Dans le sud de la Réserve, les populations de Tométi-Kondji, chassées une première fois en 1977, sont revenues en 1992. Elles ont été de nouveau obligées de partir mais ont laissé les traces de leur passage. Des fourrés denses présents dans les zones perturbées témoignent de la recolonisation forestière après l’abandon des zones de cultures. L’emplacement de ces zones de cultures correspond aux zones forestières existantes en 1949. En cinquante ans (1949–1998), près de la moitié des forêts ont disparu avec un rythme annuel très impressionnant. Ces forêts ne représentent plus que 4 479 ha constituées en 97 fragments forestiers. Leur rythme de disparition est estimé sur l’ensemble de la Réserve à 56 ha/an entre 1949 et 1979 et 101 ha/an entre 1979 et 1998 (tableau 2).

Diversité floristique de la RFT

L’inventaire floristique a permis de dresser une liste totale de 485 espèces végétales dans 182 relevés. Les 485 espèces

Tableau 2 – Vitesse de disparition de la forêt dans la Réserve et sa zone périphérique.

Zone 1: terroir de Gbohoulé; zone 2: terroir de Dédé; zone 3: terroir de Tométi-Kondji.

Vitesse de disparition (ha/an)	Forêt	
	1949-1979	1979-1998
RFT	56	101
Zone 1	37	9
Zone 2	4	13
Zone 3	81	1

recensées dans la RFT sont regroupées en 83 familles et 317 genres. Pour l’ensemble de la Réserve, les familles d’Angiospermes les mieux représentées sont les Légumineuses (35 espèces de Fabaceae, quinze espèces de Mimosaceae et onze espèces de Caesalpiniaceae), Rubiaceae (35 espèces) et Euphorbiaceae (27 espèces). La flore rencontrée dans les îlots forestiers est composée de 350 espèces réparties en 75 familles et 251 genres. Dans ces fragments de forêts, les familles les mieux représentées sont les mêmes que celles qui dominent la flore globale de la RFT à savoir les Légumineuses (24 espèces de Fabaceae, onze espèces de Mimosaceae et huit espèces de Caesalpiniaceae), Rubiaceae (27 espèces) et Euphorbiaceae (23 espèces).

Dans les recrûs forestiers, les espèces rencontrées se répartissent en 59 familles et 169 genres. Les familles qui y sont les mieux représentées sont les Légumineuses (Fabaceae (22 espèces), Caesalpiniaceae (huit espèces) et Mimosaceae (six espèces)). Les espèces rencontrées en savanes se répartissent en 57 familles et 160 genres. Les familles les mieux représentées sont les Légumineuses [Fabaceae (24 espèces), Caesalpiniaceae (dix espèces) et Mimosaceae (huit espèces)], Rubiaceae (quatorze espèces) et Poaceae (douze espèces).

L’ensemble des relevés (485 espèces × 182 relevés) soumis à l’Analyse Factorielle des Correspondances (AFC) permet de distinguer trois lots (fig. 3). Les deux axes de l’AFC totalisent une inertie de 27,65%. L’axe 1 (20,23% de l’inertie)

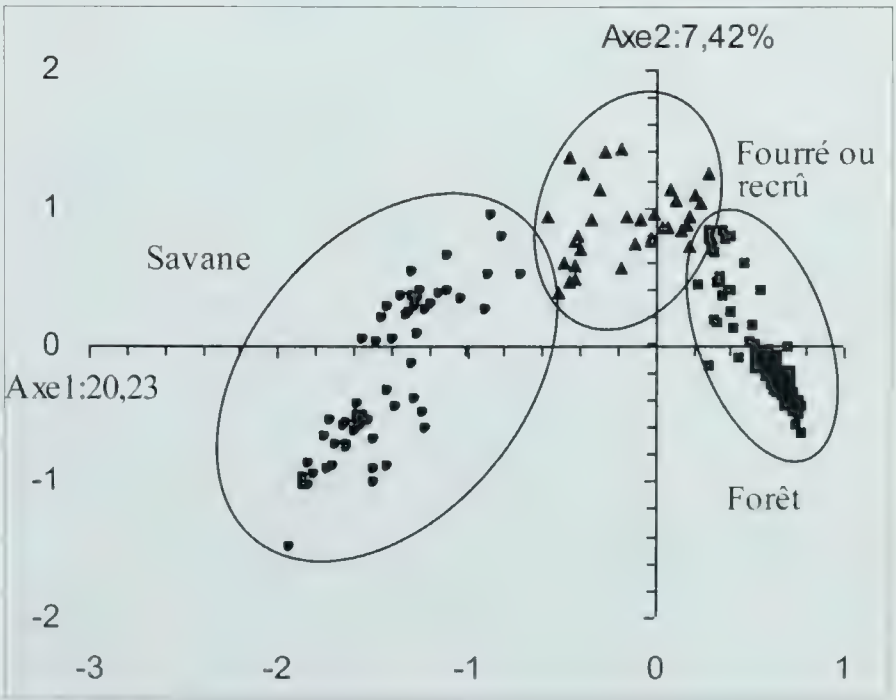


Figure 3 – Répartition des formations végétales dans les deux premiers plans de l’Analyse Factorielle de Correspondance.

Tableau 3 – Indice de diversité floristique dans la Réserve.
N_o = richesse spécifique; I_{sh} = Indice de Shannon; Eq = équitabilité.

Indices de diversité	Diversité moyenne sur l'ensemble de la RFT	Fragments de forêt	Recrûs forestiers	Savanes	F	P
N _o /ha	183 ± 38	205 ± 34	154 ± 21	129 ± 19	F _{28;3} = 8,70	10 ⁻³
I _{sh}	6,97 ± 0,32	7,14 ± 0,20	6,71 ± 0,24	6,33 ± 0,30	F _{28;3} = 11,02	10 ⁻³
Eq	0,93 ± 0,01	0,93 ± 0,00	0,92 ± 0,01	0,78 ± 0,01	F _{28;3} = 13,37	10 ⁻³

sépare les relevés en forêts de ceux réalisés en savanes. L'axe 2 (7,42% de l'inertie) met en évidence les recrûs forestiers. Cette discrimination des relevés est due à la spécialisation de certaines espèces recensées dans cette aire protégée. En effet, 350 espèces sont propres aux fragments forestiers, 225 espèces recensées dans les recrûs forestiers et fourrés sur termitières disséminées en savane et 206 espèces recensées en savane dont 132 sont propres à cette formation végétale. Des espèces communes (soit 158 taxons) peuvent se retrouver dans les trois formations végétales (fragments de forêts, recrûs forestiers et savanes).

Comme l'indiquent les résultats ci-dessus, les fragments de forêt concentrent une importante diversité floristique par rapport aux autres types de formation végétale (recrûs forestiers et savanes). En effet, les indices de diversité montrent que les valeurs calculées, en particulier la richesse spécifique (N_o) et l'indice de Shannon (I_{sh}) sont supérieures aux valeurs moyennes sur l'ensemble du site (tableau 3). Si ces valeurs ne sont pas significativement supérieures aux valeurs moyennes sur l'ensemble de la Réserve, elles le sont par rapport aux savanes et aux recrûs forestiers. Seules les savanes présentent une équitabilité moyenne significativement inférieure (F_{28;3} = 13,37; P < 0,001), montrant que les espèces forestières sont mieux représentées dans les îlots et les recrûs forestiers. La savanisation accrue de la végétation de la RFT est une perte de la biodiversité locale car les fragments de forêt conservent plus de diversité floristique (tableau 3).

DISCUSSION

Dynamique de la couverture forestière dans la Réserve de faune de Togodo

L'analyse de l'évolution de la couverture végétale dans la RFT à cinquante années d'intervalle (1949 à 1998) indique une tendance globale à la régression des surfaces forestières. Cette régression s'estime à 44,67% de la superficie de l'aire protégée entre 1949 et 1998. Cette tendance à la régression des surfaces forestières constatée n'est pas singulière à la RFT. Elle s'apparente à l'évolution générale de l'ensemble de la couverture forestière du pays avec un taux de régression forestière évalué à 4,5% pour la période 2000–2005 (FAO 2007). Aussi, les travaux de Adjou et al. (2010a) dans la Réserve de faune d'Abdoulaye au centre du Togo ont montré que les changements d'affectation et d'utilisation des terres dans cette aire protégée entre 1972 et 2000 se caractérisent par une diminution des superficies des formations forestières (-1,29%) et des savanes arborées (-1,70%) au profit de la savane arbustive (+1,77%) et des zones de culture et de jachères (+1,12%). Cette régression des formations forestières est également constatée par d'autres auteurs dans la sous-région

(Adomou 2005, Hountodji 2008, Youta 1998). En effet, les résultats de l'analyse des modifications et évaluation de la dégradation du couvert végétal dans les zones sahélienne et soudanienne de l'Afrique de l'Ouest révèlent une diminution importante des zones boisées et de la végétation en général (Hountodji 2008). De même, les travaux de Dixon et al. (1996), indiquent qu'entre 1970 et 1990, les surfaces forestières du Cameroun et du Ghana ont considérablement diminué avec respectivement, une moyenne annuelle de 0,6 et 1,3%. Les études conduites par la FAO de 1990 à 1995, montrent que les plus forts taux annuels de dégradation des forêts et autres espaces boisés africains sont observés en Afrique de l'Ouest notamment dans les pays comme le Togo (1,44%), Ghana (1,26%), le Bénin (1,25%), la Guinée (1,12%), la Gambie (0,86%), et le Nigeria (0,86%) (FAO 1995).

Cette étude montre également que la fragmentation forestière est bien réelle au niveau des forêts togolaises et s'observe sur le terrain ou par analyse des photographies aériennes et par imagerie satellitale. Les résultats révèlent que le degré de fragmentation des îlots forestiers de la Réserve a considérablement augmenté entre 1949 et 1979. Elle s'est beaucoup accentuée entre 1979 et 1998 entraînant la disparition pure et simple de certains fragments forestiers et leur reconversion en zone de cultures. L'emplacement de certaines zones de cultures actuelles correspond à celui d'anciens fragments de forêt encore visible sur la carte de 1949. D'autres recherches récentes ont également souligné la perte considérable des habitats forestiers tropicaux autour et à l'intérieur des aires protégées avec pour conséquence l'isolement croissant des habitats écologiques (DeFries et al. 2005, Clerici et al. 2007). Les travaux de Clerici et al. (2007) basés sur l'utilisation des données satellitaires à haute résolution, ont établi une tendance d'isolement des complexes écologiques dans la W-Arly-Pendjari (WAP) en Afrique occidentale. Ces auteurs ont estimé que plus de 14,5% de l'habitat de savane a été perdue dans les zones périphériques du WAP, alors que 0,3% a été converti à l'intérieur du complexe. L'accentuation de ce processus de fragmentation forestière pourrait réduire la probabilité de la survie de certaines espèces ou entraîner la diminution de la taille des populations et même accroître le risque d'extinction des espèces vulnérables (Clerici et al. 2007).

Cependant, la régression forestière telle que décrite dans cette étude n'est pas partout admise. Fairhead & Leach (1998) ont montré que la mise en culture autour d'îlots forestiers en zone péreforestière de la Guinée favorisait l'extension de la forêt. Sur le plateau d'Akposso au sud-ouest du Togo, où la pluviométrie est nettement supérieure à celle de la plaine côtière, Guelly (1994) signalait que les jachères de savanes évoluent en forêt lorsque les conditions d'exploita-

tion changent et passent des cultures de plein champ à des cultures sous couvert. Ces conditions favorables à l'extension de la forêt sont loin d'être rassemblées dans la plaine côtière du sud du Togo.

Cette tendance générale à la régression des superficies forestières est principalement expliquée par des actions anthropiques (intrusion des populations dans la forêt pour l'agriculture, feux de brousse criminels, coupes frauduleuses, etc.). Ainsi, à l'intérieur de la Réserve, près de 21% de la superficie forestière a été reconvertie en espace agricole et on n'y observe plus que des pieds de *Ceiba pentadra* dominant des surfaces mises en cultures. La FAO signale que ces défrichements massifs sont intervenus dans cette zone entre 1969 et 1979 (FAO 1980). En effet, la dynamique démographique et agricole de la population dans les localités environnantes constitue le premier facteur responsable de la régression forestière. Entre 1949 et 1979, le défrichement dans la zone périphérique de la Réserve est tellement fort que toutes les formations forestières existant sur la zone 3 (terroir de Tomety-Kondji) ont été éliminées. Les fourrés à *Mallotus oppositifolius*, présents dans la zone perturbée de la Réserve, témoignent de la dynamique forestière après l'abandon des zones mises en cultures par les populations. Les autres formes de pressions identifiées dans la zone en périphérie de la RFT sont le braconnage et la pêche, l'exploitation forestière, les autres activités humaines engendrées par la croissance démographique, les feux de brousse incontrôlés et la récolte des produits forestiers non ligneux (UICN/PACO 2008). Les défrichements, les coupes de bois, la cueillette ont une grande importance socio-économique autour de la RFA parce qu'ils constituent une source de revenus indispensable pour de nombreuses familles. Cette forte pression a entraîné une modification dans la structure et la physionomie des îlots de forêt (Kokou et al. 1999). Salzmann & Hoelzmann (2005) ont aussi estimé que le taux élevé de dégradation de la végétation du Bénin et du Togo peut être imputable aux causes climatiques car les deux pays sont situés dans le couloir du Dahomey qui a été considérablement influencé par les changements climatiques de l'Holocène.

Par ailleurs, les politiques agricoles mises en œuvre au cours de ces périodes, n'ont pas été en adéquation avec les priorités de conservation des ressources forestières et ont entraîné par conséquence l'accentuation du processus de dégradation des ressources forestières de la RFT et de sa zone périphérique. En effet, la période de plus forte régression des superficies forestières (22% entre 1971 et 1979), coïncide avec les grands projets agricoles qui ont donné lieu à la création de plusieurs institutions chargées de former et d'encadrer les paysans notamment la Société Togolaise de Coton (SOTO-CO) créée en 1974. En 1976, la 'Révolution Verte' fut lancée et prône l'autosuffisance alimentaire pour tous les togolais. Mais à côté, aucune politique environnementale n'a été élaborée pour parer aux méfaits de cette révolution agricole. C'est en cette période que de grandes portions de forêt juxtaposant la partie septentrionale de la RFT ont cédé la place aux champs de coton et d'autres cultures vivrières. A cet effet, pour l'avenir, une concertation entre les différentes instances en charge des domaines forestier et agricole est indispensable puisque les problèmes liés à la déforestation sont intimement liés aux méthodes agricoles extensives. Une gestion concer-

tée d'un espace permet justement l'association des compétences forestières et agricoles.

Il faut noter que la méthode utilisée pour l'analyse diachronique du couvert végétal dans la RFT et sa zone périphérique au cours de cette étude a eu quelques limites. En effet, quelques difficultés sont intervenues, dues aux déformations lors du scannage des transparents, à des imprécisions lors du géoréférencement de l'image et à des différences de la nature même de la base d'observation (image satellite/photos aériennes) et de leur échelle (1/30 000^e pour 1979, 1/50 000^e pour 1949 et 1998). Ces difficultés ont introduit un biais dans le calcul des superficies et pourrait entraîner une surestimation des valeurs trouvées pour le calcul des superficies notamment celles des années 1949 et 1979. L'erreur relative entre les valeurs calculées avoisine globalement 6%.

Conservation de la biodiversité dans la Réserve de faune de Togodo

L'intérêt particulier des fragments de forêt de la Réserve de faune de Togodo dans la conservation de la diversité biologique au plan national se traduit par l'existence dans cette aire protégée d'espèces 'clés' dont les indices de rareté sont pour la plupart très élevés. Au cours des prospections botaniques effectuées dans la Réserve, 485 espèces végétales ont été recensées dans 182 relevés, ce qui représente 14% environ de la flore du Togo estimée à environ 3 491 espèces végétales. Le nombre d'espèces recensées dans cette Réserve est relativement inférieur à celui trouvé par Adomou (2005) qui a énoncé 561 espèces dans 167 relevés floristiques au cours des travaux similaires à la même latitude au Sud du Bénin. Sur le nombre total d'espèces recensées dans la Réserve, 350 espèces (soit 72,16% du nombre total d'espèces végétales inventoriées) sont propres aux fragments forestiers. Ce qui indique que ces fragments de forêt concentrent une importante diversité floristique par rapport aux autres types de formation identifiés dans l'aire protégée. Ces îlots de forêts semi-décidues à faciès sec ont été également décrits au Bénin comme faisant parti des sites à forte concentration d'espèces végétales exclusives et menacées (Adomou 2005).

Parmi les espèces recensées, 18 taxons ont été récoltés pour la première fois au Togo (appendice électronique) car n'étant pas encore signalés dans la flore du Togo (Brunel et al. 1984) ni dans les mises au point qui ont suivi son édition (Akpagana 1992, Akpagana & Guelly 1994). De plus, certains de ces nouveaux taxons sont des espèces exclusives à la Réserve de Faune de Togodo notamment *Balanites wilsoniana*, *Schrebera arborea* et *Strychnos usambarensis* (tableau 4). Ces espèces exclusives n'ont pas encore été signalées dans aucune autre formation forestière du pays (Courcelaud 2002, Sogoyou 2010, Adjonou et al. 2010b). Elles se caractérisent également par un indice de raréfaction supérieur à 80%, c'est-à-dire qu'elles peuvent être considérées comme des espèces en danger dont les formations forestières de Togodo constituent les derniers refuges au Togo. D'autres espèces recensées dans la Réserve sont classées sur la liste rouge de l'UICN dans la catégorie des espèces rares, en danger critique ou vulnérables (UICN 2001) (tableau 4). Toutes ces catégories d'espèces pourraient disparaître du territoire si ces sanctuaires de biodiversité venaient à disparaître (Adjo-

Tableau 4 – Espèces en danger conservées dans la Réserve.
EX, espèce exclusive à la RFT; EN, en danger; CR, en danger critique; VU, vulnérable.

Espèce	Famille	RI (%)	Statut IUCN
<i>Capparis viminea</i> Hook.f. & Thomson ex Oliv.	Capparaceae	99,45	VU
<i>Monanthotaxis parviflora</i> Verdc.	Annonaceae	99,45	EN
<i>Phyllanthus bellei</i> Hutch.	Euphorbiaceae	99,45	CR
<i>Strychnos usambarensis</i> Gilg	Loganiaceae	99,45	EX
<i>Lannea welwitschii</i> (Hiern) Engl.	Anacardiaceae	98,90	EN
<i>Lasiodiscus mildbraedii</i> Engl.	Rhamnaceae	98,90	EN
<i>Pycnocomia angustifolia</i> Prain	Euphorbiaceae	98,90	CR
<i>Oxyanthus subpunctatus</i> (Hiern) Keay	Rubiaceae	98,35	EN
<i>Ventilago diffusa</i> (G.Don) Exell	Rhamnaceae	98,35	CR
<i>Dovyalis afzelii</i> Gilg	Flacourtiaceae	97,80	CR
<i>Balanites wilsoniana</i> Dawe & Sprague	Zygophyllaceae	97,25	EX
<i>Hymenostegia afzelii</i> (Oliv.) Harms	Caesalpiniaceae	96,70	EN
<i>Schrebera arborea</i> A.Chev.	Oleaceae	95,05	EX
<i>Gongronema angolense</i> (N.E.Br.) Bullock	Asclepiadaceae	91,20	EN
<i>Croton nigritanus</i> Scott-Elliot	Euphorbiaceae	90,65	EN
<i>Ritchiea duchesnei</i> (De Wild.) Keay	Capparaceae	85,71	EN
<i>Chaetacme aristata</i> Baker	Ulmaceae	78,02	VU
<i>Dennettia tripetala</i> Baker f.	Annonaceae	76,92	EN

nou et al. 2010b). Compte tenu de toutes ces considérations, les fragments de forêts conservés dans la Réserve de faune de Togodo peuvent être identifiés comme faisant parti des sites prioritaires de conservation de la biodiversité du Togo.

Les résultats de cette étude montrent que dans les pays à faible couvert forestier comme le Togo, des écosystèmes forestiers et des espèces en voie de disparition sont encore conservés dans les aires protégées. C’est l’exemple des fragments de forêt semi caducifoliée à faciès sec identifiés dans cette étude et qui sont homologues à la ‘dry semi-deciduous forest’ décrit par Hall & Swaine (1981). Fairhead & Leach (1998) signalent que ceux qui soutiennent la thèse de déboisement exagéré dans le couloir du Dahomey, ont vu en ces îlots de forêt, les vestiges d’une ancienne forêt continue sur toute la côte. Cependant, les espèces rares, en danger critique ou menacées d’extinction qui sont encore présentes dans ces fragments forestiers peuvent être indicatrices de l’état du fonctionnement de ces écosystèmes, et peuvent être le signe de la dégénérescence imminente de la biodiversité dans cette partie du Togo.

Malgré le rôle important que jouent ces fragments de forêt dans la conservation de la biodiversité forestière dans cette partie très anthropisée de la côte togolaise, plusieurs éléments menacent leur existence. En effet, les nombreuses pressions que subissent ces formations forestières provoquent leur fragmentation et hypothèquent sérieusement leur existence. La fragmentation de ces écosystèmes constitue de ce fait la plus grande menace pour la conservation de la diversité biologique qu’ils regorgent. Par ailleurs, le projet de construction du barrage hydroélectrique à Adjarala par les Etats togolais et béninois sur le fleuve Mono constitue une menace pour la conservation de la biodiversité dans cette Réserve. Sogoyou

(2010) a estimé qu’environ 2 550 ha de savane et 145 ha de forêt seront ainsi submergés par la retenue qui serait constituée de part et d’autre du fleuve Mono et de ses affluents. La même source indique que la perte de la biodiversité végétale et animale qui sera associée à la disparition des écosystèmes forestiers risque d’être grave si aucune mesure n’est prise concernant les espèces exclusives, rares et menacées inféodées à cette Réserve. Ainsi la disparition de ces espèces à valeur écologique importante disqualifierait la RFT par rapport à son statut actuel de Parc National de ressources naturelles car non seulement l’extinction de ces espèces importantes diminueraient les populations des espèces végétales de la forêt mais surtout causeraient une crise écologique par rapport à la convention des Nations-Unies sur la diversité biologique (McNeely 1995, Balmford et al. 2005).

Cette étude fournit également des éléments essentiels pour tester les indicateurs écologiques et la validité scientifique de certains critères et indicateurs proposés pour la gestion durable des forêts tropicales africaines (OAB-OIBT 2003, OIBT 2005) à savoir le critère 3 sur la santé de l’écosystème forestier et le critère 5 sur la diversité biologique (OIBT 2005). L’analyse floristique effectuée à partir des données d’inventaires a permis de décrire des éléments de la biodiversité végétale (composition floristique, espèces exclusives, rares, en danger et vulnérables) et d’établir que cette Réserve regorge encore d’un grand potentiel en espèces végétales. Aussi, les résultats obtenus constituent-ils d’importantes bases techniques pour l’identification des zones particulièrement menacées et l’évaluation de l’état de conservation de la diversité biologique dans ces milieux. Ils permettent ainsi de répondre aux deux principaux objectifs de la Convention sur la Diversité Biologique notamment “L’évaluation de l’état de conservation de la diversité biologique et l’identification des

zones particulièrement menacées des terres arides et sub-humides” (CBD 2001). Aussi, la Convention sur la Diversité Biologique a souligné depuis 1992 que des mesures doivent être mises en œuvre pour la conservation des écosystèmes naturels, en particulier pour les forêts tropicales, car ces dernières regorgent des écosystèmes les plus riches en espèces sur la planète (CBD 2002). Pour le cas des fragments de forêt de la RFT, la première démarche consiste à la sécurisation des limites de cette Réserve c’est-à-dire, matérialiser effectivement et de façon consensuelle les limites périphériques de la Réserve (Principe 2, Critère 2.2; OAB-OIBT 2003) afin d’éviter des intrusions des populations pour l’installation de nouvelles cultures. Le renforcement des actions de sensibilisation et d’échange d’idées entre les différents acteurs (services étatiques, ONG, populations) dans l’optique d’une gestion participative serait favorable à la pérennité de l’aire protégée de Togodo.

CONCLUSION

L’analyse de l’évolution de la couverture végétale dans la RFT à cinquante années d’intervalle (1949 à 1998) indique une tendance globale à la régression des surfaces forestières (44,67% de la superficie de l’aire protégée entre 1949 et 1998). Cette régression s’est beaucoup accentuée entre 1979 et 1998 entraînant la disparition pure et simple de certains fragments forestiers et leur reconversion en zone de cultures. Cette tendance générale à la régression des superficies forestières est principalement expliquée par les actions anthropiques (intrusion des populations dans la forêt pour l’agriculture, l’exploitation forestière, le braconnage, les feux de brousse incontrôlés, la récolte des produits forestiers non ligneux, etc.) et quelquefois par les changements climatiques. Ces îlots forestiers se fragmentent de plus en plus entraînant la disparition de certains îlots et leur reconversion en des zones de culture. Leur rythme de disparition est estimé sur l’ensemble de la Réserve à 56 ha/an entre 1949 et 1979 et 101 ha/an entre 1979 et 1998.

L’analyse floristique effectuée à partir des données d’inventaires a permis d’établir que cette Réserve regorge encore d’un grand potentiel floristique avec un cortège floristique de 485 espèces, ce qui représente environ 14% de la flore du Togo. Sur ce nombre total, 350 espèces (72,16% du nombre total d’espèces végétales inventoriées) sont propres aux fragments forestiers traduisant une importante diversité floristique dans ces fragments de forêt. Parmi les espèces recensées, 18 espèces sont nouvelles à la flore du Togo car n’ayant pas encore signalés dans cette flore ni dans les mises au point qui ont suivi son édition. De plus, certains de ces nouveaux taxons (*Balanites wilsoniana*, *Schrebera arborea* et *Strychnos usambarensis*) sont des espèces exclusives à la Réserve de faune de Togodo. D’autres espèces recensées sont classées sur la liste rouge de l’UICN dans la catégorie des espèces rares, en danger critique ou vulnérables. Toutes ces catégories d’espèces pourraient disparaître du territoire si ces sanctuaires de biodiversité venaient à disparaître. Compte tenu de toutes ces considérations, les fragments de forêts conservés dans la Réserve de faune de Togodo peuvent être identifiés comme faisant parti des sites prioritaires de conservation de la biodiversité du Togo.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible au format Excel sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> > SBB50 > dossier 455) et consiste en une liste des taxons recensés lors des relevés floristiques.

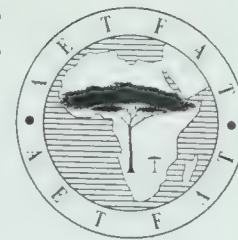
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Manuscript received 28 May 2010; accepted in revised version 9 Dec. 2010.

Communicating Editor: Elmar Robbrecht.



Ecological survey of the Lycophytes and Ferns of the Vohimana Reserve, Madagascar

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Background and aims – The Malagasy Vohimana Reserve, is situated in an ecologically sensitive area subject to mining and the pressure from neighbouring communities. The aim of this study is to look at the structure of the plant community, to determine indicator species of undisturbed areas and areas affected by human activities, and to present a checklist of ferns and lycophytes of the reserve.

Methods – The Vohimana Reserve was visited twice and an improved quadrat method of sampling was used; specimens were collected and identified at both TAN and P herbaria. Ecological data were statistically analysed using the Factorial Correspondence Analysis methods.

Key results – One hundred and thirty two lycopod and fern taxa were identified, including four undescribed fern species. The plant community structure suggests a gradation from primary forest to disturbed zones. This can be explained by local ecological factors and topography, as well as the effect of human pressure on the plant community. The narrow altitudinal gradient (780–1,030 m) is not considered as a factor influencing species composition, as shown in analogous studies performed in larger parks or reserves elsewhere in Madagascar.

Conclusion – Despite the human impact on the reserve, the fern and lycophyte diversity indices suggest that it should be classified as an area of significant diversity.

Key words – ferns, lycophytes, diversity, Madagascar, Vohimana Reserve, conservation, biological indicators.

INTRODUCTION

About 85% of the fern and lycophyte diversity is concentrated in tropical areas, especially in mid-elevation cloud forests (Smith et al. 2006, Mehlreter 2008). Too often neglected in ecological studies and taxonomic inventories, ferns and lycophytes form an important component of tropical hygrophilous ecosystems, where they frequently dominate the understory and the epiphytic component. In the palaeotropics, ferns represent one of the most important epiphytic plant groups, making up 36 to 72% of this flora (Benzing 1990, Dubuisson et al. 2009). Epiphytic fern diversity and quantity is also known to be the first to decline when forest ecosystems are disturbed (Hoff & Cremer 1993, Barthlott et al. 2001, Dubuisson et al. 2005). Currently there are 586 lycophyte and fern species known from Madagascar, including 265 endemic species (47.32%) (Rakotondrainibe 2009).

The Vohimana Reserve, 150 km east of Antananarivo, is located in one of Madagascar's biodiversity hot-spots (Vences et al. 2009, Dolch 2009). This reserve is managed by the Malagasy Non-Governmental Organisation “*L'homme*

et l'environnement” (“*Man and environment*”), and the study was conducted in the framework of the biodiversity programme of the NGO (<http://www.madagascar-environnement.com/strategies-de-programme.html>) with the aim of increasing knowledge on the reserve required for its management. This has become necessary due to the ongoing anthropogenic pressures (farming, mining, and the construction of a pipeline) in the area. Approximately 1,200 self-sustained people live in the area and use the traditional unsustainable slash and burn (‘tavy’) method of cultivation, which is repeated after two years of fallow laying (five years being the minimal duration for nutrient turn-over). The large community does not allow the complete regeneration of the forest. In addition, the construction of a 220 km long pipeline that will carry nickel and cobalt rich laterites from Ambatovy (30 km west of Vohimana) to Toamasina harbor is underway. For this development a road was constructed from the Ambavani-asy village to the future pipeline. The effect of this mining project has not been determined, but the loss of biodiversity will probably be high. Human activities have shown to drastically decrease plant biodiversity in the region: after 48

years of forest recolonisation following deforestation and agricultural activities, less than 25% of the native plant diversity has recovered in the Malagasy Andasibe region (Dolch 2009). Given the current pressure on the reserve, a fern and lycophyte inventory will contribute to the knowledge of the forest diversity before mining exploitation.

Apart from developing a checklist of the ferns and lycophytes of the Vohimana Reserve, studies were conducted to determine the ecological factors explaining fern and lycophyte distribution with the aim of using these plants as indicators to monitor the impact of human activities.

One of the NGO's projects is to restore the forest corridor between the Mantadia National Park (north of Vohimana) and the Vohimana Forest, with native species. As a result of the sensitivity of ferns and lycopods to disturbance (Dubuisson et al. 2005) they can potentially be used as additional ecological indicators when assessing and monitoring the effect of forest disturbance.

MATERIAL AND METHODS

Vohimana is a rural area, 150 km east of Antananarivo (electronic appendix 1A). The area covers 1,635 ha, including a forest core of 600 ha. Settlements are established along the perimeter of the area. The Vohimana Forest is divided by the Vohitra and Sahatandra Rivers and is further fragmented by human activities (electronic appendix 1B).

The study site is composed of environments that include patches of agricultural lands, fallow lands, *savokas* (recolonised bush), and exploited tropical humid forests (electronic appendix 1C).

Species inventories were conducted in July 2006 and April 2008, corresponding respectively to the dryer winter season (July) and the end of the rainy season (April).

Sampling protocols and data management proposed by Rakotondrainibe & Raharimalala (1996) and applied in several studies (Rakotondrainibe & Raharimalala 1996, 1998, 2000, Rakotondrainibe 2000, 2002, 2003), especially in forests within the same phytogeographical zones (Rakotondrainibe & Raharimalala 1998, 2000), were followed.

Based on a vegetation and landscape study of the reserve (Buron 2004), and our own observations, five vegetation types are recognized within the study area:

Dense primary evergreen and wet rain forests – this plant community has not been exposed to excessive human activity, but can be selectively exploited for wood harvesting and hunting.

Herbaceous fallow – defines the first stage of abandoned farmland.

Shrubby fallow (*savoka*) – fallow grassland to shrub up to five meters high.

Secondary or exploited forest – this vegetation type includes forest variously utilized for wood harvesting as well as recolonized forest after the shrubby fallow stage. Several stages of recolonisation can be identified, each being characterized by a specific plant community. When trees are dominant in the plant community, different developmental stages are not distinguished. It is often difficult to distinguish between recolonised and exploited forests.

Eucalyptus plantations – these forests have been established 1925 in and have since been used for timber and the charcoal industry.

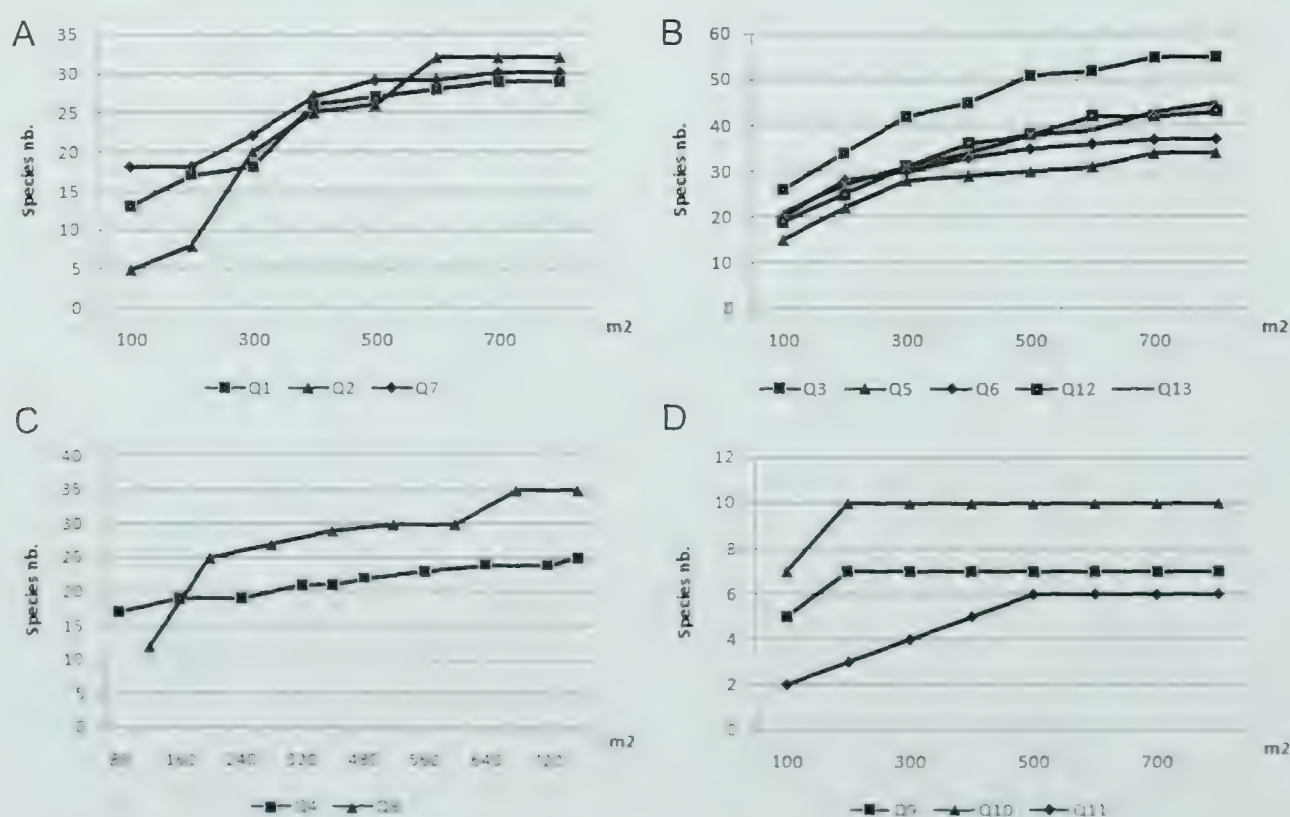


Figure 1 – Species-areas curves for plots, grouped by topographic zone. A, Top-hills and high slopes plots. Q1 stands in a secondary forest. Q2 and Q7 stands in primary forest riverbanks. B, Mid-slopes plots in humid primary forest. Q5 is in an exploited forest. C, River-banks plots. Q4 stands along frequented secondary forest riverbanks, Q8 stands along humid primary forest riverbanks. D, Fallows plots. Q9 and Q10 lie in flat and open bottom slopes with stagnant water. Q11 stands in a dry and mid slope.

Table 1 – Endemism in other similar malagasy forest (Centre and East province) for Pteridophytes (from Rakotondrainibe 1998, 2000).

Forest name	Surface	Altitude (m)	Number of species	Endemism	Year of prospecting
Ambohitantely	1,600 ha	1,300–1,650	154	25.3%	2000
Andranomay (Anjozorobe)		1,300–1,450	130 (in only 6 days, 150 estimated)	31.5%	1998
Vohamina (this study)	1,635 ha (600 ha of forest)	780–1,030	132	34.09%	2006 and 2008

Study areas were selected to represent the topographical and vegetation diversity (electronic appendices 2 & 1D). Plots of 800 m² were selected following Rakotondrainibe & Raharimalala (1996). Species number curves support the plot size as maxima area reached between 100 m² (fallow communities, fig. 1D : Q9, Q10) and 700 m² (primary evergreen and wet rain forest, fig. 1B) plots. Figure 1A & D represent hill top and river bank plots. Each plot was established within a homogeneous vegetation. The 800 m² plots were surveyed using eight contiguous sub-plots of 100 m². The choice of sub-plots was determined by the topography of the site and the necessity of a homogeneous habitat. Each sub-plot was explored through transect surveys in both directions.

All fern and lycophyte species were recorded. For unknown taxa a voucher specimen was collected for later identification. Growth form, phenology and number of individuals were recorded for each plot. Individual plants were identified with ease in species with short rhizomes and clustered fronds. In species with long-creeping rhizomes, each frond was considered as an individual since individual plants could not be identified. Small epiphytic ferns (Hymenophyllaceae and Polypodiaceae, incl. Grammitidaceae) were recorded as a colony when individual rhizomes could not be distinguished and where plants cover an area of 400 cm²; when rhizomes could however be identified they were counted and each rhizome was scored as a colony.

This survey method is not entirely satisfactory since it may overvalue creeping terrestrial ferns and undervalue the smaller epiphytic species with creeping rhizomes.

Vouchers collected in the 2006 survey were deposited at the Laboratoire de Biologie Végétale, Faculté des Sciences, Mahajanga University, Madagascar. Vouchers collected in 2008 will be deposited at the National Herbarium (P), Paris, France, while duplicates will be deposited at the National Herbarium of Tsimbazaza (TAN), Antananarivo, Madagascar.

Identifications were based on the Flora of Madagascar (Tardieu-Blot 1951, 1952, 1958a, 1958b, 1971), Zahamena Park inventory (Rasolohery 2003), African fern floras (Burrows 1990, Verdcourt 1999a, 1999b, 2006, Schelpe 1970, Schelpe & Anthony 1986, Roux 2003), as well as a number of monographs (Hennipman 1982, Holttum 1974).

Family and genera, apart from the families Hymenophyllaceae and Cyatheaceae, *Elaphoglossum* and *Lastreopsis* follow Kramer (1990). Ebihara et al. (2006) was followed for the Hymenophyllaceae, Rouhan (2005) for *Elaphoglossum*, Janssen & Rakotondrainibe (2007, 2008) for *Cyatheaceae*,

and Rakotondrainibe & Tronchet (2009) for *Lastreopsis*. Smith et al. (2006) was followed in arranging the fern families. Name updates follow Roux (2009).

Abundance classes were attributed using to the following parameters: 1: a single individual or colony; 2: 2–4 individuals or colonies; 3: 5–9 individuals or colonies; 4: 10–19 individuals or colonies; 5: 20–49 individuals or colonies; 6: 50 or more individuals or colonies.

For each plot a diversity index was calculated using the Shannon-Weaver Index (Peet 1974). The same protocol was followed in 2008, allowing specific richness comparisons using the index H'_{spec} .

$$H'_{spec} = \sum (p'_i \cdot \ln p'_i)$$

where p_i is the relative frequency of the species i , evaluated for a maximum of 400 individuals (8 sub-plots and 50 individuals maximum for a sub-plot). This index gives a value lower than that of the Shannon-Weaver Index.

A plot/ecological factor matrix (ACM) was developed using mixed quantitative factors (altitude, slope and canopy height) and qualitative factors: vegetation type (fallow and savoka, primary forest, secondary forest), topography (lower slopes, river banks, mid-slopes, hilltops and upper slopes), slope orientation, presence of water (no water in the plot, stagnant water, stream or river). The analysis was conducted using the R *ade4* package (Thioulouse et al. 1997, Dray & Duffour 2007).

To evaluate the structure of the fern communities, a species frequency/plot matrix was constructed (112 species × 13 plots) and analyzed by Factorial Correspondence Analysis (FCA). The analysis compares species distribution among plots and maximizes the proximity of individual variables (species or plots). Each cell (i, j) of the matrix is weighted by a χ^2 calculation and the individual variables of the weighted matrix are projected on a plan defined by two axes representing the first two factors of importance, explaining the variance. The origin is the center of gravity of the cloud of points. The distribution of points, according to each axis projected, is correlated to the ecological gradient. Close points are interpreted as demonstrating correlation among the considered factors. The R *ade4* package (Thioulouse et al. 1997, Dray & Duffour 2007) and *dudi.coa* command were used to treat the species/plots matrix.

Only species that contributed at least 1.8% of the variance for one or more axis are represented in the FCA projection graphs. Fifty-one representative species were kept, and

Table 2 – Comparison of growth form between Ambohitantely and Andranomay-Anjozorobe forest and Vohimana reserve for the fern flora.

E = epiphytes; ER = epiphytes and saxicolous; T = terrestrial; TR = terrestrial and saxicolous; R = saxicolous.

Growth form	Vohimana	Ambohitantely	Andranomay
E + ER	59.09%	27.30%	43.80%
T+ TR	37.12%	60.40%	44.60%
TE	3.79%	7.10%	8.50%
R	-	5.20%	3.10%

as argued by Rakotondrainibe & Raharimalala (2000), “they represented the most characterized species, excluding species that are too widely distributed, those that are infrequent, and those whose distribution is erratic”. The same species number is used in both the check-list and graph to describe the species distribution.

A Hierarchical Classification based on the floristic matrix using the R package *Vegan* (Dixon 2003) and the distance method *Canberra* was established, retaining four clusters.

The hierarchical classification and the FCA based on the same floristic/plot matrix were compared.

RESULTS

One hundred thirty-two (132) lycophyte and fern taxa were recorded within the study area (electronic appendix 3). A few taxa (< 5% of the collected specimens) were not identified to species level (especially Cyatheaceae), because numerous collections were sterile or incomplete. These collections were not incorporated in the analysis. The H_{spev} for each plot is reported in electronic appendix 4A. Fallow plots (Q9, Q10, Q11) were least diverse whereas primary wet forest plots (Q3, Q12, Q13) were the most diverse.

Forty-five lycophyte and fern taxa (34.09%) recorded for the Vohimana Reserve are Malagasy endemics (Rakotondrainibe 2009). The occurrence of endemic lycophytes and ferns in this reserve is slightly higher than in other Malagasy reserves (table 1).

Growth form studies (table 2) show that most taxa are epiphytic (59.09%), followed by terrestrial (37.12%) species.

3.79% of the species are facultative epiphytic, but mostly terrestrial. *Pteris madagascariensis* may have a climbing habit, but the only true liana is *Lygodium lanceolatum*, a heliophilous fern found in fallow areas, forest margins, or forest openings.

In fallow plots *Lygodium lanceolatum* mostly climbs on ferns such as *Pteridium aquilinum* and *Dicranopteris linearis*. In forest plots (Q7 & Q13, see electronic appendix 2) where the herbaceous stratum is not well developed, *Lygodium* occurs as isolated populations. This may be the result of old forest clearings, or chablis.

Plot classification based on ecological factors (ACM) – Three axes contribute 63.1% of the variance (fig. 2). The parabolic form of the graph is a result of the ecological gradient (Guttman-effect), opposes, on the first axis, low elevation plots, exposed to full sun (Q9, Q10 and Q11) and largely harbouring herbaceous plants, to steep, mid-slope plots with the highest and densest canopy. Conditions that most likely affect species diversity are light intensity and a stable high humidity (Q3, Q5, Q13, Q12). Hill top plots (Q1, Q2, Q7) are also located on the negative part of the first axis. The lower canopy of these forests and the more frequent occurrence of *Pandanus* trees result in an increase in light intensity.

Plots Q4 and Q8 are both riverbank plots and make a more significant contribution towards axis 3 than other plots (fig. 2B). Larger rivers cause in a break in the forest canopy allowing sunlight to reach the forest floor for the greater part of the day. Running water is present in these plots only (except for two small streams crossing Q3 and Q12, but here the canopy is uninterrupted). Rocks and bare soil along riv-

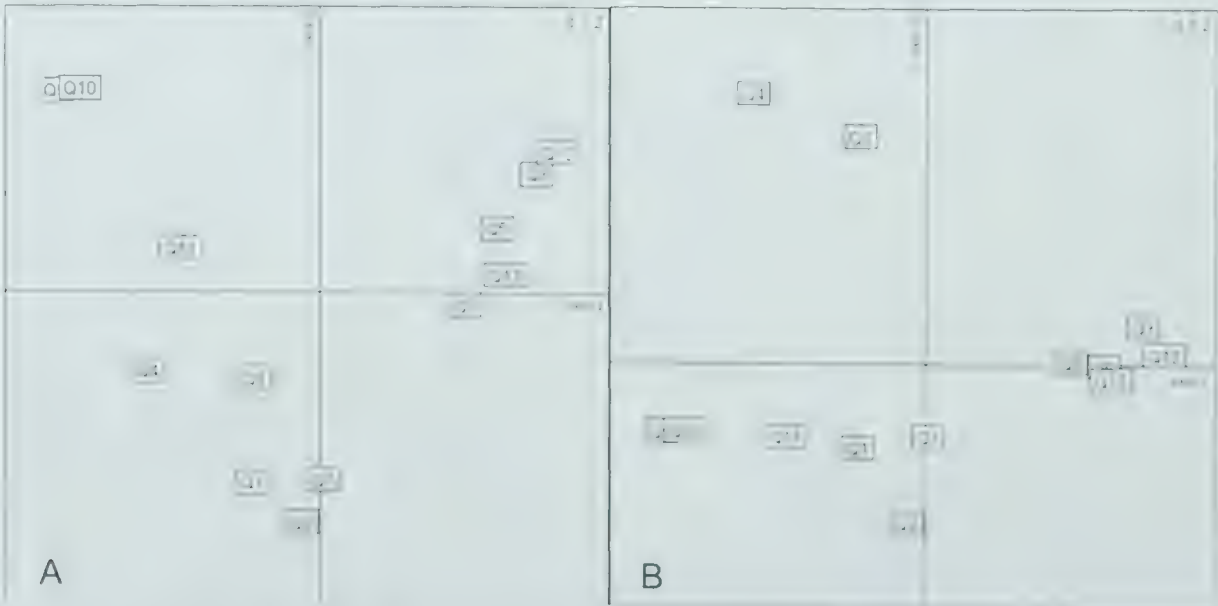


Figure 2 Multivariate analysis (ACM) of the thirteen plots expressed in function of ecological factors. A, for axes 1 and 2; B, for axes 1 and 3.

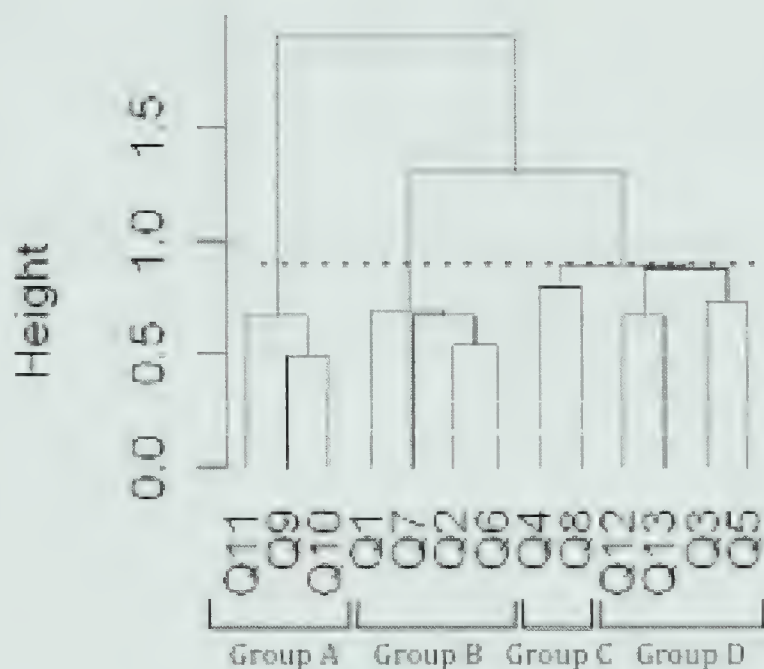


Figure 3 – Hierarchical analysis using Canberra method for matrix analysis and ward method for tree construction of the thirteen plots, based on their fern floristic frequency analysis.

ers contrast with the deep and thick humus rich soils located along the undisturbed lower hill slopes. Fallow plots on flat areas also benefit from the natural movement of humus from higher lying areas.

This survey confirms the existence of different ecological niches among plots.

Hierarchical classification of the floristic frequency matrix analysis – The tree obtained by the plot/floristic analysis is divided in order to obtain four groups (fig. 3). The plot groups can be characterized as: Group A = fallow plots (Q9, Q10, Q11); Group B = hill top plots (Q1, Q2, Q7) and high-middle slope plots (Q6); Group C = river bank plots; Group D = primary wet forest plots (Q3, Q5, Q12, Q13). River bank plots (Group C) appear to be related to Group D (primary wet forest plots).

Four axes were retained for the FCA analysis, projecting the plot/fern frequencies matrix. The analysis accounts for 60.12% of the global variance. The fourth axis is difficult to

interpret, but provides interesting information for some fern species, and was thus kept. To make the figures more readable, the variable (plots and species) projection graphs are separated. Each axis reflects the data provided in electronic appendix 4B.

Plot projection – Axes 1 and 2 are plotted in fig. 4A; axes 1 and 3 in fig. 4B; and axes 1 and 4 in fig. 4C. The contribution of each plot towards each axis is provided in electronic appendix 4C.

On axis 1, fallow plots (Group A) are grouped, suggesting a significant similarity in the fern species composition. These plots make a larger contribution towards the axis (electronic appendix 4C) than other plots, except Q4 (disturbed river bank). Fallow plots share a more open vegetation, free of trees and are subject to constant sunshine.

Axis 2 compares hill top plots (Group B) river bank plots (Group C). Hill top plots are characterized by a low forest canopy, small-diameter trees, a dominance of crowded *Pandanus* trees and bamboo lianas. The low canopy allows light to reach the ground more freely. River bank plots occur in primary wet forest at mid- or lower-slopes. These plots have a higher canopy due to the taller trees that may also occur along the river banks.

Axis 3 compares river bank plots (Q4, Q8) which stand in a relatively isolated position. Plots Q12 and Q13 (part of primary wet forest plots) and fallow plots are on the positive part of axis 3. The central position of hill top plots does not allow a precise interpretation for these plots.

For axis 4, the plot opposition (Q8, Q3, Q12 versus Q13, Q7, Q4) can be explained by an orientation effect, or a very local effect: Q8, Q3 and Q12 are on the same northern slope and quite close to each other (see electronic appendix 1C).

Species projections – When the fern species are projected (fig. 5), indicator or typical ferns for each group become evident. A synthesis of the fifty-one characteristic species and their typical habitat contributes at least 1.8% to one or more axes as reported in electronic appendix 5. An ordinated table based on the FCA on the 112 species and the thirteen plots

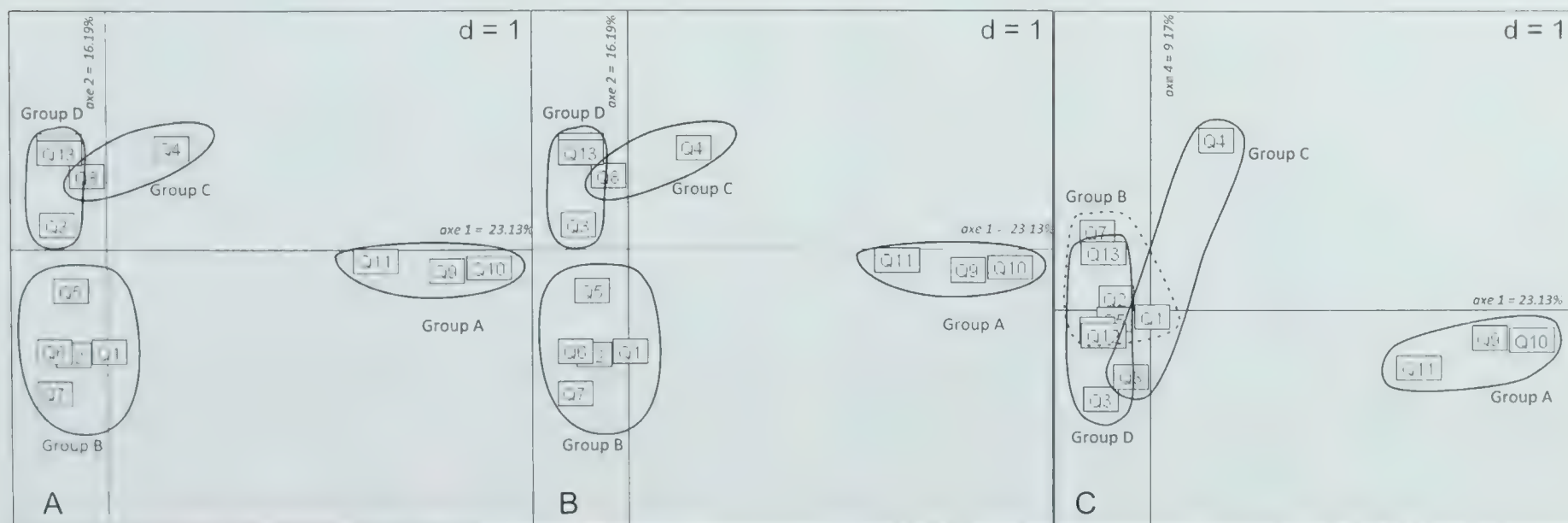


Figure 4 – Plot projection according to Factorial Correspondence Analysis (FCA) of the thirteen plots against 112 fern species matrix frequency. Group A = plots in fallows; Group B = hill top and high-slope plots; Group C = river banks plots; Group D : Mid-slopes in FI (primary forest) A, for axes 1 and 2; B, for axes 1 and 3; C, for axes 1 and 4.

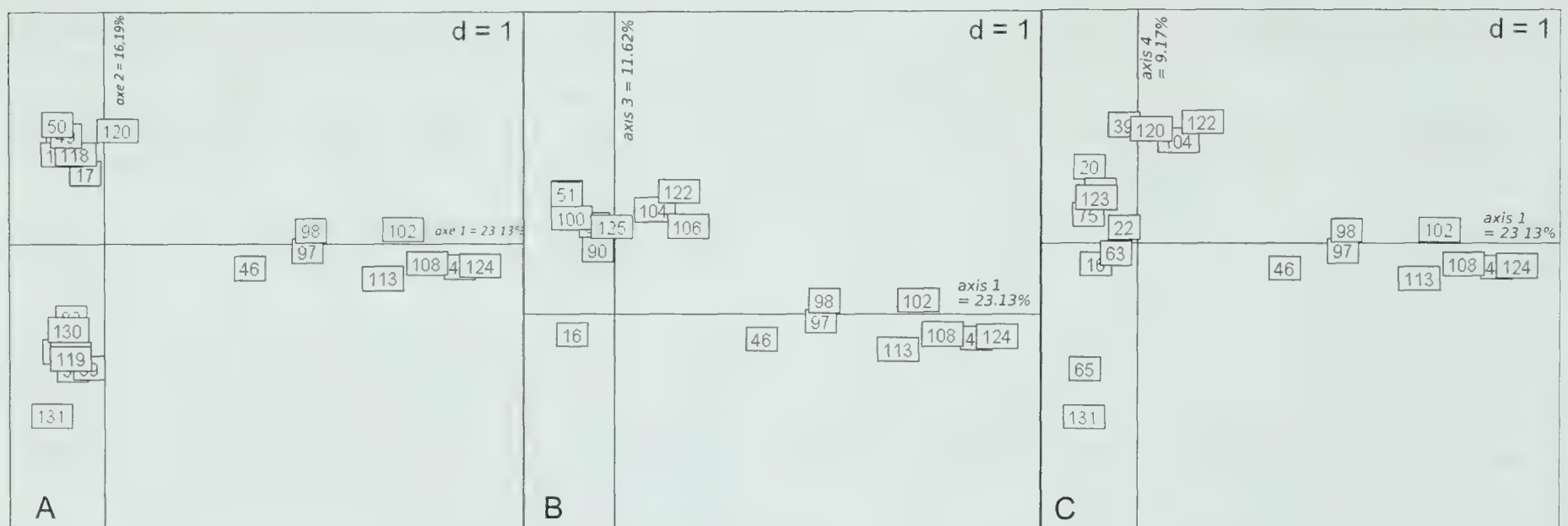


Figure 5 – Factorial Correspondence Analysis (FCA) of the thirteen plots against 112 fern species matrix frequency. Only ferns contributing for at least 1,8% of the variability for one or two axes are shown. Labels correspond to those reported in the check-list (electronic appendix 3. A, for axes 1 and 2; B, for axes 1 and 3; C, for axes 1 and 4.

completes this analysis (electronic appendix 6) and shows ordinated distribution of the whole community among plots.

On axis 1, species occurring in fallow areas plots are in the positive part. Included here are species such as *Pteridium aquilinum*, *Cheilanthes viridis* and *Lygodium lanceolatum*. The river bank fern flora grows on a moist substrate (Rasolohery 2003), in a sunny or lightly shaded areas and include *Osmunda regalis* and *Sphaerostephanos arbuscula*. They all plot on the positive part of axis 1.

Axis 1 clearly separates species and plots with different light requirements. Shade-loving species of primary humid and closed canopy forest plots (*Antrophyum boryanum*, *Didymoglossum montanum* (= *Trichomanes montanum*), *Didymoglossum rotundifolium* (= *Trichomanes rotundifolium*), *Saccoloma henriettae*) all occur along the negative part of axis 1. In plot Q1, positioned on a hill top and at the edge of an ancient fallow area, where light penetrates more than in closed plots, some open space fern species are found. These sun species are the only ferns encountered in fallow plots (Q9, Q10, Q10) (*Lycopodiella cernua*, *Pteridium aquilinum*) (Rasolohery 2003) (see electronic appendix 6).

Dwarf *Didymoglossum* species (leaves not exceeding a few centimeters in length) are also projected on the positive part of axis 2 (fig. 5A), and characterize shade-loving hygrophilous taxa. On the negative part of this axis 2 we find species such as *Cochlidium serrulatum* (= *Xiphopteris serrulata*) and *Schizaea dichotoma*. The latter is characterized by tough leaves with a thick cuticle illustrating xerophilous adaptation. They were principally collected on hilltops as also reported in other inventories (Rasolohery 2003). They are often exposed to full sun. Axis 2 separates hill top species and lower slope forest species. Correlated with the topographic gradient, there are changes in microclimate such as ambient humidity and light intensity.

Axis 3 (fig. 5B) more or less separates terrestrial species such as *Osmunda regalis*, *Sphenomeris chinensis* and *Odontosoria melleri* found in open area, along pathways, on lateritic soils and along river banks. At the opposite, *Belvisia spicata*, *Antrophyum boryanum*, *Asplenium dregeanum* are

epiphytic species found in closed canopy forests and lower hill slope areas (Rasolohery 2003).

DISCUSSION

Microclimate influences the ecology and diversity of species in a forest community. Rakotondrainibe & Raharimalala (2000) demonstrated an increase in epiphytism with a rise in humidity and/or altitude. In the Vohimana forest, epiphytes are more common when compared with the Ambohitantely forest or Andranomay forest (table 2). The infrequency of rocks or boulders in Vohimana, except along river banks explains the small number of epilithic or saxicolous species (6.15%). *Pellaea angulosa*, *Odontosoria melleri*, *Pityrogramma calomelanos* were observed on rocks along the river banks. *Pityrogramma calomelanos* also occurs on rocky embankments along the railway line. *Didymoglossum lenormandii*, *Polyphlebium borbonicum* and *Hymenophyllum digitatum* are concentrated along the river banks or in very humid and shady plots. Plants in these locations are dependent on water flow over the rocky face (for Hymenophyllaceae). *Pityrogramma* spp. exhibit more xerophytic features.

It is not surprising that fallow plots have the lowest diversity index, and that the primary wet forest plots the highest (electronic appendix 4A). Secondary or exploited forests show an intermediate index. In each topographical situation, the plots affected by man display the smaller number of species and smaller H'_{spec} index. As noted by Barthlott et al. (2001), ferns are one of the first plant groups to disappear when forests are disturbed. Human activity leads to a significant decrease in species diversity and leads to a homogenization of the fern communities in open areas following tavy cultivation. Only well adapted ferns and lycophyte species survive in full sun and relatively dry areas. These species are often invasive and usually cover large areas (*Pteridium aquilinum* and *Lycopodiella cernua*).

Light intensity plays a major role in the variation of fern diversity within communities. Sunlight is highest in exposed areas, but decreases from secondary forests and up-hills forests to closed canopy primary forests. Exposed sites may

Table 3 – Sørensen similarity between Ambohitantely and Andranomay-Anjozorobe forest and Vohimana reserve for the fern flora.

	Ambohitantely	Andranomay-Anjozorobe
Number of shared species with Vohimana	46	51
Total number of species	154	131
Sørensen similarity coefficient	0.32	0.40

be the result of natural disturbance (tempest, chablis) or to anthropogenic actions. In further analysis ecological factors such as light intensity and duration, rainfall and humidity as well as humus type and thickness should be determined using more accurate measurement devices than possible for this study. Additional data are needed for some taxa (especially Cyatheaceae) in zones such as *Eucalyptus* plantations, rocky riverbanks, and open areas along the Vohimana River not yet explored.

Other factors may also contribute to canopy opening: soils are leached after deforestation over large areas (Drew 1983, Gade 1996), and large forest gaps in a forest dry the ambient atmosphere (Canham et al. 1990), even in tropical regions with a high rainfall.

When natural openings in the forest canopy occur, they can form an enriched mosaic of abiotic conditions in a relatively small area. They also contribute to the natural rejuvenation of forests with light tolerant and terrestrial species establishing in a short time. Vegetation formation is also dependent on topography and influence fern diversity according to the structure of the trees (canopy height, tree size, biological type). *Pandanus* or bamboo stands on hilltops and upper slopes do not carry epiphytic species. This may explain the lower diversity of the fern flora of hill top plots (electronic appendix 4A). The larger contribution of hill top and river banks plots and the smaller contribution of fallow plots of fallow plots to axes 2, 3, 4 (electronic appendix 4C) support this conclusion. The loss of an epiphytic flora in areas influenced by human activity is due to the decrease of large diameter trees and their absence in exploited forest and fallows. The large contribution of Q4 to the axis 3 of the plots projection can be interpreted by its mixed features: an undisturbed river bank, a disturbed river bank, and a dense secondary forest overhanging an undisturbed riverbank.

Bare soil can also result from the natural flow of rivers, preventing humus deposition on rocky soil along the rivers, preventing perennial species from establishing in these areas.

Many studies on fern diversity and ecological distribution have been conducted in the Malagasy reserves (Rakotondrainibe 2009). The pteridophyte (lycophytes and ferns) flora of Madagascar is very diverse due to the variation in climate, topography, geology, and vegetation and many mountain ranges harbour a group of unique species. The most comparable forests already surveyed for ferns are the Andranomay-Anjozorobe forest (Rakotondrainibe 1998) and the Ambohitantely forest (Rakotondrainibe 2000). Both are

mid-elevation wet forests in the Central Plateau and belong to the same phytogeographical zone, the Center Domain. The three forests are located along an East (Vohimana) – West (Andranomay and Ambohitantely) transect. The Sørensen similarity coefficient shows that the Vohimana Forest fern community is closer to the Andranomay-Anjozorobe community than it is to the Ambohitantely community (table 3). The endemism rate is also higher in Vohimana Forest (34.09%) than that in Ambohitantely, (25.3%) and Andranomay-Anjozorobe (31.5%) (table 2). Fern endemism for the island is 45.2% (Rakotondrainibe 2009, Rakotondrainibe et al. 1996) and 37.4% for the Center Domain. These values are close to the endemism rate in Vohimana Forest.

This relatively well preserved Vohimana forest community requires a detailed management plan that makes provision for the needs of the local population in a sustainable manner. Despite the relatively small area covered by relict primary forest, the overall fern diversity in Vohimana is still significant when compared with other Malagasy parks and reserves. An analysis of the fern community shows a drastic loss in biodiversity when the primary forest is disturbed.

In the Andasibe region, the forest is still very fragmented forest (electronic appendix 1B), and the Vohimana reserve plays a major role, not only because of its natural biodiversity, but also because of the investment of a local NGO and populations in reforestation actions. But the pipeline crossing the Vohimana forest is a very negative offsets of the sustainable development efforts. The current vegetation formations with high diversity will be replaced with very low diversity secondary formations. It is still very necessary to support all the protection actions of these primary formations.

SUPPLEMENTARY DATA

Supplementary data are available in pdf format at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consists of the following: (1) maps of the Vohimana reserve and its surroundings; (2) characteristics of the selected plots in the Vohimana reserve; (3) check list of ferns and lycophytes in the Vohimana Reserve; (4) specific diversity index and inertia; (5) fifty-one representative species of the Vohimana reserve, for the four biotopes defined by their floristic composition; (6) ordination table of the species repartition.

ACKNOWLEDGEMENTS

We want to thank: the Malagasy and French students who participated to the fields trips: Macha Bardin, Cheri Christian Totondrabesa, Mathieu de Flores, Elise Dumax, Aurélie Grall, Faharidini, Donald Nantenaina, Rova Rabevahiny, José Tsarasonina, Orlane Salvadori, Léa Tarallo. LeSabotsy, guide at Vohimana Forest, whose botanical knowledge and experience helped a lot in our survey; the French naturalist association “Timarcha” which has supported the 2006 field trip and has allowed French students to discover the tropical forest; the NGO “L’homme et l’environnement” and its manager / founder, Olivier Behra and all the Malagasy people from the NGO who facilitated our surveys. Special thanks

to Tahiana Andriahaimalala who helped organizing the material and fieldwork; the “Madagascar National Parks”, who gave authorizations for this study, and Mme Lalao Andriamahefarivo from the Missouri Botanical Garden, who facilitated administrative requirements; France Rakotondrainibe, Muséum National d’Histoire Naturelle, who helped with fern identifications and contributed through constructive remarks; Germinal Rouhan, Muséum National d’Histoire Naturelle, who helped with *Elaphoglossum* identifications; Cyril Gallut, UPMC, who helped with computer management; Elisabeth Blanchon for English corrections; reviewers and editor to have accepted this manuscript and for their pertinent remarks which permitted to improve it.

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Manuscript received 3 Aug. 2010; accepted in revised version 2 Nov. 2011. This paper was pre-published on 1 Nov. 2012 in issue 145(3) of *Plant Ecology and Evolution*.

Communicating Editors: Sylvain Razafimandimbison & Thomas Janssen.



Impact of livestock grazing on forest structure, plant species composition and biomass in southwestern Madagascar

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Background and aims – To contribute towards a better understanding of habitat utilization by livestock and its impact on biodiversity components in the dry ecosystems of Madagascar.

Location – Southwestern Madagascar, in and around Tsimanampesotsa National Park.

Methods – We quantified species composition, life forms, structure, and plant biomass of different vegetation formations in areas of four different grazing intensities: (1) ungrazed for four years prior to the study, (2) grazed by zebu during the dry season, (3) grazed by zebu at the end of wet season and during the dry season, and (4) grazed by goats during the wet and the dry season and by zebu at the beginning of the dry season. The food biomass available was compared with the food biomass required.

Key results – Zebus feed on the east side of the National Park during the wet season as long as there is enough water in that area. When water becomes scarce, the zebus return to the western side of the park. Goats are restricted to the littoral zone in the west year-round. As a result, goats and zebus occupy different proportions of the various vegetation types of our study area. Zebus also use the littoral forest, but only at the end of wet and during the dry season. Large parts of the spiny bush on the limestone massif and dry forest on ferruginous soil are not used regularly by zebus. Plant species richness and diversity varied in relation to grazing pressure and soil conditions. In the littoral and on red sand, plant diversity decreased with grazing pressure. This change was most pronounced in the littoral zone. Since grazing pressure increases during the dry season, grazing affects mostly woody species, since herbs are no longer available during the dry season. In contrast to the bush encroachment due to grazing in Africa, grazed areas in southwestern Madagascar contain fewer woody plants and plant species than areas not used by livestock.

Key words – Forest-pasture, transhumance, grazing effect, fodder biomass, Tsimanampesotsa National Park.

INTRODUCTION

In most dry regions of the world, livestock represents a very important source of income and insurance against variation in agricultural production due to climatic unpredictability and erratic rainfall (Riginos & Hoffman 2003, Dickhoefer et al. 2010). The dry regions of Madagascar are no exception. In many parts of Madagascar grazing leads to the degradation of the natural ecosystems. While the degradation of forest and non-forest ecosystems due to grazing seems obvious in many parts of south and southwestern Madagascar, quantitative data on livestock carrying capacity and indicators for degradation or overgrazing are not available (ANGAP et al. 1999, Mahazotahy 2006). This lack of information hinders the establishment of a monitoring program for habitat quality

and the implementation of a management plan for sustainable land use that reconciles the need for livelihoods of the human population and conservation of Madagascar's unique ecosystems.

Southwestern Madagascar is a prime example where livestock is a most important cultural and economic component (Sourdat 1970, Pannoux 1991, Razanaka et al. 2001, Rakotoarison 2005, SuLaMa 2011) embedded in biologically unique ecosystems that are under high pressure from human land use (Fenn 2003). Stockbreeders in southwestern Madagascar face several problems. First, the region is characterized by a long dry period with irregular rainfall including years without rain. The insufficient water supply reduces the range of cattle as the dry season progresses. Since cat-

tle have to stay close to water, more distant areas are grazed only lightly with substantial amounts of plant biomass remaining at the end of the wet season (Bosser 1954). Second, the pasture is dominated by herbaceous species of low forage value, such as *Cenchrus ciliaris*, *Panicum pseudovoeltzkowi*, *Eragrostis cilianensis* and *E. pilosa* (Bosser 1954, Morat 1973). Third, parts of the pasture are transformed to agricultural land (Sourdat 1970). Forth, Madagascar is extending its protected area system, particularly forest ecosystems, thus reducing the access to forest pasture during the dry season (Borrini-Feyerabend & Dudley 2005a, 2005b).

Within this context, the goal of this study was to contribute towards a better understanding of the impact of livestock on the vegetation in the driest ecosystem of Madagascar. Within this framework, the specific objectives of this study were to: (1) document grazing impact on structural vegetation characteristics, (2) determine the impact of grazing on plant species composition, (3) identify plant species as indicators for grazing pressure, and (4) measure the biomass of fodder for livestock during different seasons.

METHODS

Site description

The study was carried out in the northern and western part of the Tsimanampesotsa National Park and at adjacent sites west of the national park. The national park is located in south-western Madagascar (24°03' – 24°12'S, 43°46' – 43°50'E) on the escarpment of the Mahafaly Plateau. The park was extended from 43,200 ha to 203,000 ha in 2007. This extension reduces access to forest pasture during the dry season. Traditionally, cattle use the forests during the dry season where they browse on woody plant species. This is considered one of the major threats to the biotic diversity of Tsimanampesotsa National Park (ANGAP et al. 1999, Goodman et al. 2002, Mahazotahy 2006). The Tsimanampesotsa NP represents Madagascar's peculiar dry and spiny forest ecosystems and covers a substantial portion of the Mahafaly Plateau. It separates extensive grassland towards the east from the littoral zone in the west. During the wet season all zebu around the Tsimanampesotsa NP are brought to the east of the Mahafaly Plateau into the region of Itomboina where extensive grass-

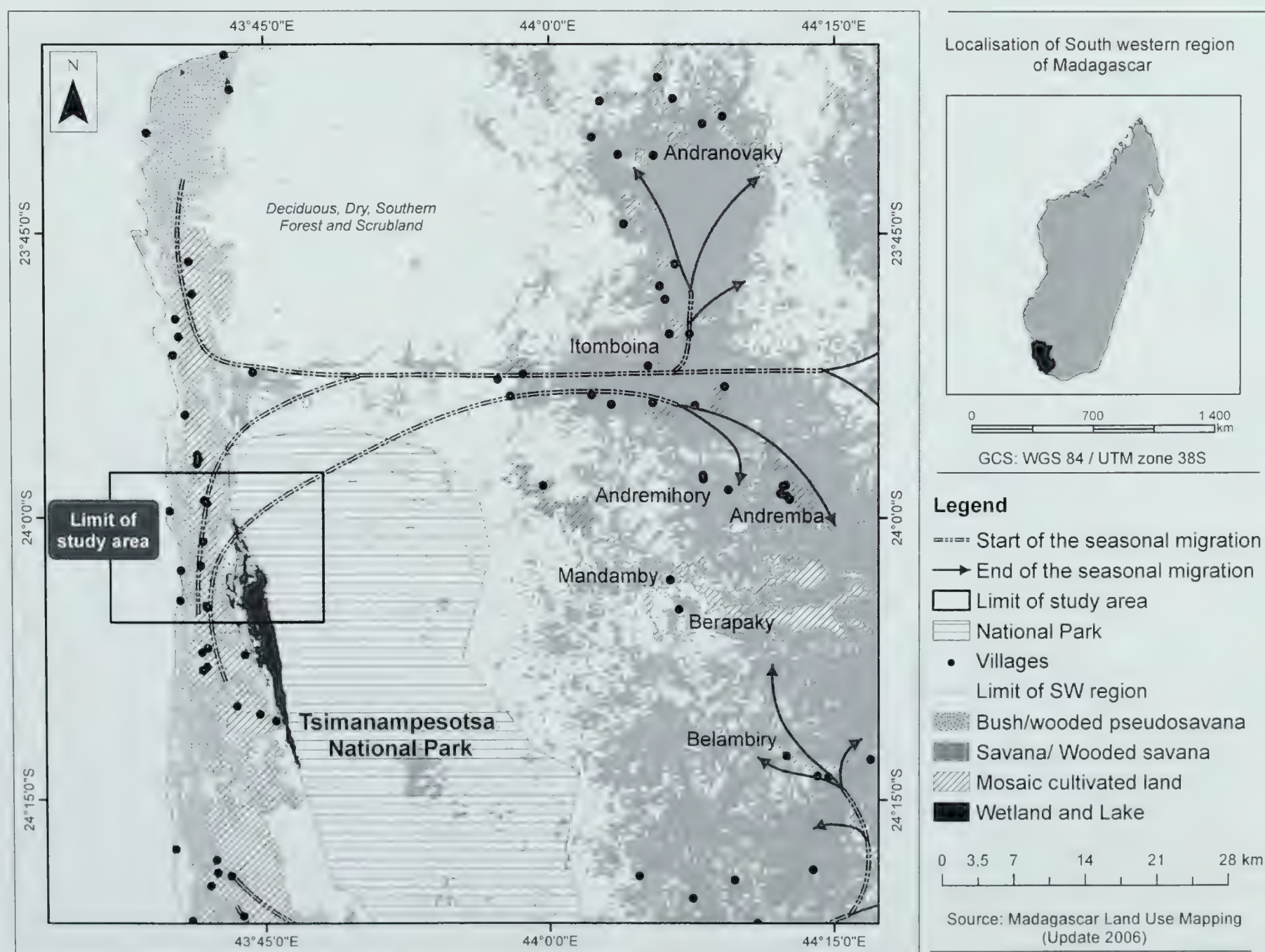


Figure 1 – Study area and seasonal migration (transhumance) of livestock between the western and eastern parts of the Mahafaly Plateau at the beginning of the wet season. The migration is reversed at the end of the wet season.

lands provide food. However, water is limited in this region. When water becomes scarce, zebus cross the limestone plateau on a traditional track of transhumance north of the Lac Tsimanampesotsa at the end of the wet season (March) even though the areas in the east still provide plenty of food. Then, cattle remain on the coastal plain where water is available year round, but food availability is low. With the progressing dry season, cattle move into the national park. They return to the east (region of Itomboina) at the end of the dry season in November (fig. 1). Goats remain in the littoral zone year round. Thus, the number of livestock west of and within the national park is highest during the dry season when herbaceous forage is not available. At this time of the year, woody plant species (liana, shrubs and trees) provide food for the animals (Le Houérou 1980).

Field research on grazing was carried out between March 2008 and March 2009. Vegetation descriptions have been performed during the wet seasons. The study is part of a more comprehensive study on the vegetation of Tsimanampesotsa NP (Ratovonamana et al. 2011).

Climate

Based on long-term averages, the region can be characterized as a semi-arid tropical climate with eight dry months (April–November) and four wet months (December–March). Months are considered ‘dry’ when rainfall (R) is less than twice the mean monthly temperature ($R < 2T$). During the dry season, the temperature varies from 17.8°C to 32.6°C and from 24°C to 35.5°C during the wet season (fig. 2). The average annual rainfall is less than 500 mm (range at Tular between 1951 and 1990: 166 – 719 mm / year; CNRE 1992), but can be irregular with ‘wet’ seasons without rain.

Vegetation

The Tsimanampesotsa forest is part of the southwestern spiny forest of Madagascar (Moat & Smith 2007). It contains some of the most unique plant communities on the island and harbors the highest level of plant endemism with 48% of the genera and 95% of the species being endemic (Elmqvist et al. 2007). The forest is characterized by many xerophytic and drought tolerant woody species of the Didiereaceae and

Euphorbiaceae. The littoral zone with sandy soil is characterized by dry forest, degraded forest and different herbaceous layers. The limestone is covered by xerophytic bush with dry forest on ferruginous soil (fig. 3). Depressions on the limestone plateau are filled with red, ferruginous soil (red sand) and covered by forest that is similar to the littoral zone. Degradation is the result of direct and indirect anthropogenic pressure, such as collection of fire and construction wood, slash and burn agriculture, fire and grazing. The different vegetation types and their phenology have been described by Ratovonamana et al. (2011).

Process of site selection

We started with an analysis of images available in Google Earth to include the full range of degradation of vegetation types, and to identify zebu trails crossing the Mahafaly plateau. True migration routes were identified on the ground. True trails were distinguished from false routes based on the presence of dung. The map and area assessment occupied by livestock have been analyzed with ArcGIS. Based on these pilot studies, we selected an area of 7591 ha for more detailed studies, located between 23°58' – 24°02'S and 43°42' – 43°47'E. Within this area, eleven sites were selected which are subject to different forms of utilization by livestock (table 1, fig. 4). The eleven sites included: dry forest on the littoral, degraded dry forest on the littoral, herbaceous formations on the littoral, dry forest on ferruginous soil, xerophytic bush on limestone, degraded xerophytic bush on limestone, bare soil and water, and herbaceous wetland formations.

Categories of grazing pressure

Since stocking rates were not known at the beginning of the study, we assigned sites to grazing intensities ranging from 1 (lowest) to 4 (highest):

- (1) Not used by livestock since 2006
- (2) Used by zebu during the dry season
- (3) Used by zebu at the end of wet season and during the dry season
- (4) Used by goats during the wet and the dry season and by zebu at the beginning of the dry season.

Floristic and structural vegetation description

We measured maximum height (in m) and trunk diameter at breast height (for trees, in cm) of woody plants within 15 × 15 m² plots. Crown diameter (Cd) was measured by projecting the edges of the crown onto the ground and measuring the diameter along two axis (maximum: Cdmax and minimum: Cdmin crown diameter axis in meters) through the crown center (Brack 1999). Crown radius (Cr) was calculated as $Cr = (Cdmax + Cdmin) / 4$. Crown volume (Cv) was calculated by using the formula for the volume of a cylinder with: $Cv = (\pi) \times (Ch) \times (Cr)^2 / 4$; Ch is the vertical extension of the crown from the first branch to the maximum height of the tree.

The herbaceous cover was estimated per species in five 1 m² subplots within each 15 × 15 m² plot following the system

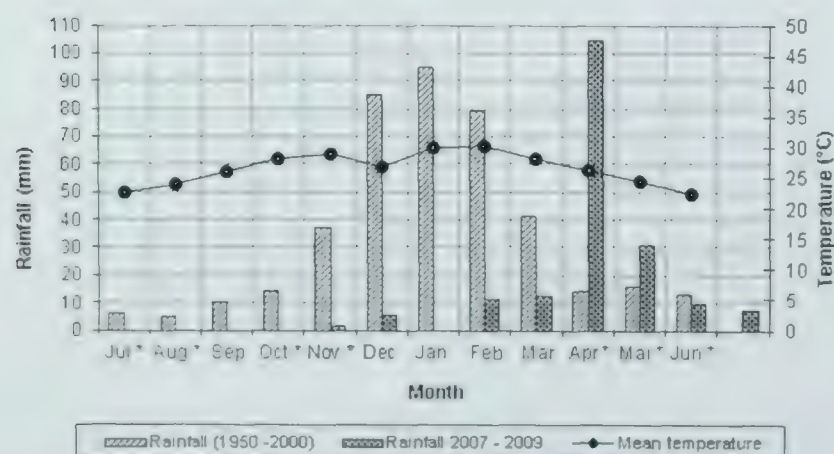


Figure 2 – Climate of the study area; (*) indicates dry months. Data from 1950 to 2000 from DIVAGIS (<http://www.diva-gis.org>). Data for the study area were recorded from 2006 to 2009 with i-buttons (temperature loggers; from Ratovonamana et al. 2011).

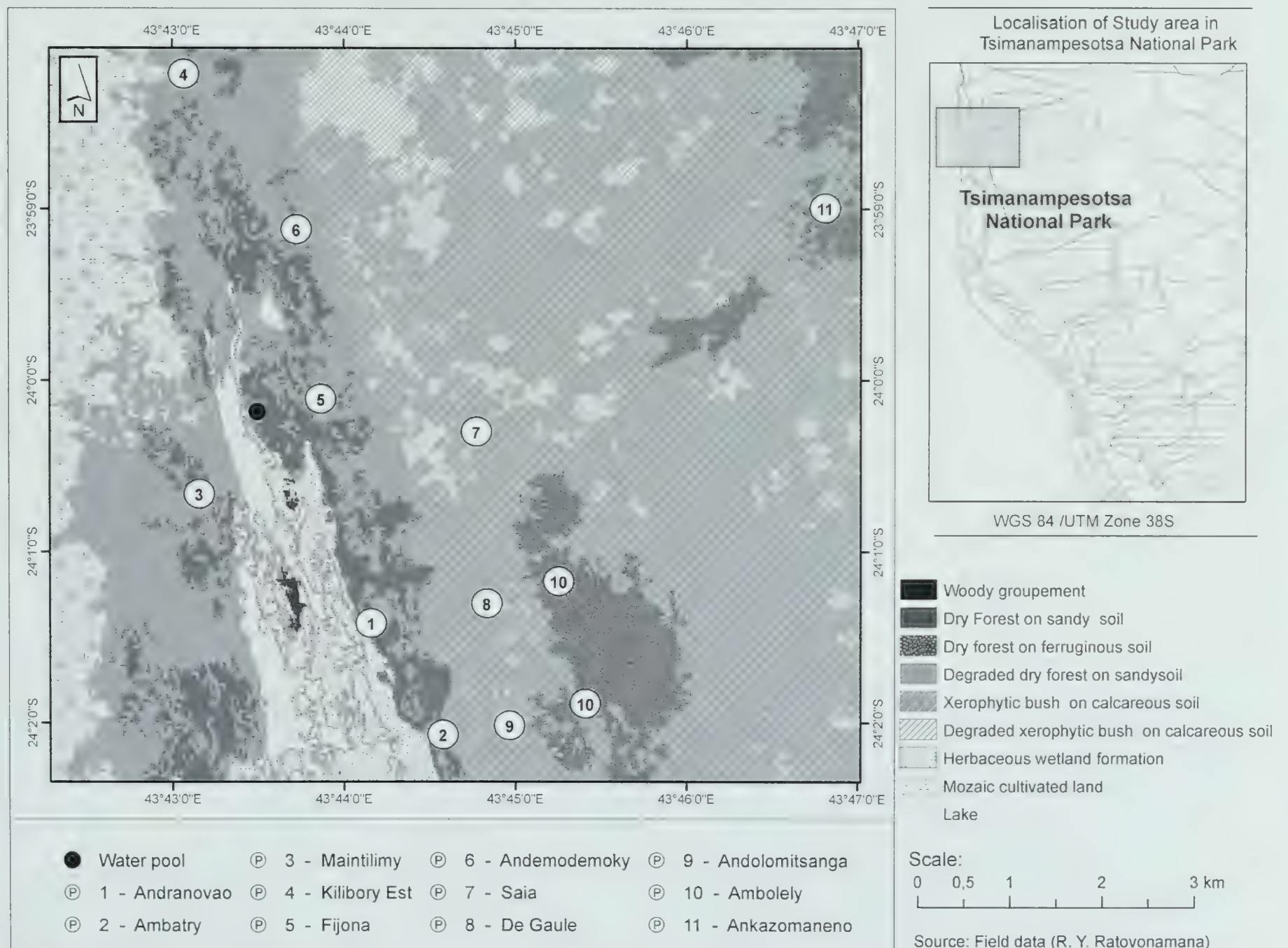


Figure 3 – Vegetation types and location of study sites in areas of different grazing regimes. Categories of grazing and site numbers are listed in table 1. Grazing pressure categories: category 1: site 1; category 2: sites 1, 2, 8, 9, 10; category 3: sites 7, 11; category 4: sites 3, 4, 5, 6.

of Braun-Blanquet. The percent coverage per species and plot was averaged for the each of the five 1 m² subplots.

Plant specimens collected in the field were identified in the herbaria of the Département de Biologie et Ecologie Végétales, FOFIFA (<http://www.fofifa.mg/>) and the Parc Biologique et Zoologique de Tsimbazaza. Since scientific names are being updated continuously, we used the names listed by Tropicos (<http://www.tropicos.org/NameSearch.aspx>). For the time being, the specimens are kept in the office of the Arboretum d'Antsokay in Toliara.

Plant species richness and plant diversity were used to characterize the effect of grazing on the different plant communities. Species diversity was evaluated using species richness (S) and specific richness (SR) (Shannon & Weaver 1949). Specific richness takes into account the number of species and the number of individuals. The similarity of plant composition for each zone under different grazing pressure was evaluated with the Spearman correlation coefficient. The relative importance of species was calculated to determine important species, considered as indicators for different forms of grazing pressure. The importance index of each

species was calculated by adding relative frequency, relative density and relative dominance (Evariste et al. 2008).

Vertical vegetation structure was used as a proxy for degradation. For this, the vegetation was subdivided in five height classes (< 25 cm, 25–49.9 cm, 50–99.9 cm, 100–149.9 cm and ≥ 150 cm) and the percentage of individuals with different life forms (tree, shrub, and liana) was measured. Detailed analyses of the vertical structure were limited to heights below 1.5 m as this is the height that can be reached by livestock in the area.

Plant biomass available as food for livestock

Since we first had to identify the most important food plant species for zebu and goats, we could not establish a rigorous sampling design to measure the productivity of the different food plant species year-round. Rather, as a first step, we identified the most important food plants for a given season and then measured their standing biomass which was available as roughage at the time the species was identified as an important food species. For woody species, we measured the crown volume of various individuals per species. Sub-

Table 1 – Study sites; vegetation formations in the littoral and on red sand are formed by dry forest.
Low spiny bush is growing on limestone (Ratovonamana et al. 2011). Classification of grazing pressure: (1) not used by livestock since 2006, (2) used by zebu during the dry season, (3) used by zebu at the end of wet season and during the dry season, (4) used by goats during the wet and the dry season and by zebu at the onset of the dry season.

Site name and site number	Number of 15 × 15 m ² plots	Categories of grazing pressure	Latitude S	Longitude E	Soil type and topography	Distance to water source (m)
Andranovao (1)	4, 4	1, 2	24°1' 25.55"	43°44' 9.21"	Sand, Littoral	2500
Ambahatry (2)	4	2	24°2' 7.61"	43°44' 35.35"	Sand, Littoral	4000
Saia (7)	4	2, 3	24°0' 19.05"	43°44' 45.02"	Limestone	2220
De Gaule (8)	3	2	24°1' 20.43"	43°44' 48.99"	Limestone	3110
Andolomitsanga (9)	2	2	24°1' 59.65"	43°44' 55.25"	Limestone	4220
Ambolely (10)	10	2	24°1' 31.80"	43°45' 30.48"	Read sand	4000
Maintilimy (3)	7	4	24°0' 41.79"	43°43' 10.10"	Sand, Littoral	1600
Kilibory (4)	4	4	23°58' 14.02"	43°43' 3.28"	Sand, Littoral	3600
Fijona (5)	10	4	24°0' 7.69"	43°43' 50.45"	Sand, Littoral	600
Andemodemoky (6)	5	4	23°59' 7.44"	43°43' 43.07"	Sand, Littoral	1900
Ankazomaneno (11)	9	3	23°59' 0.62"	43°46' 47.78"	Read sand	5900

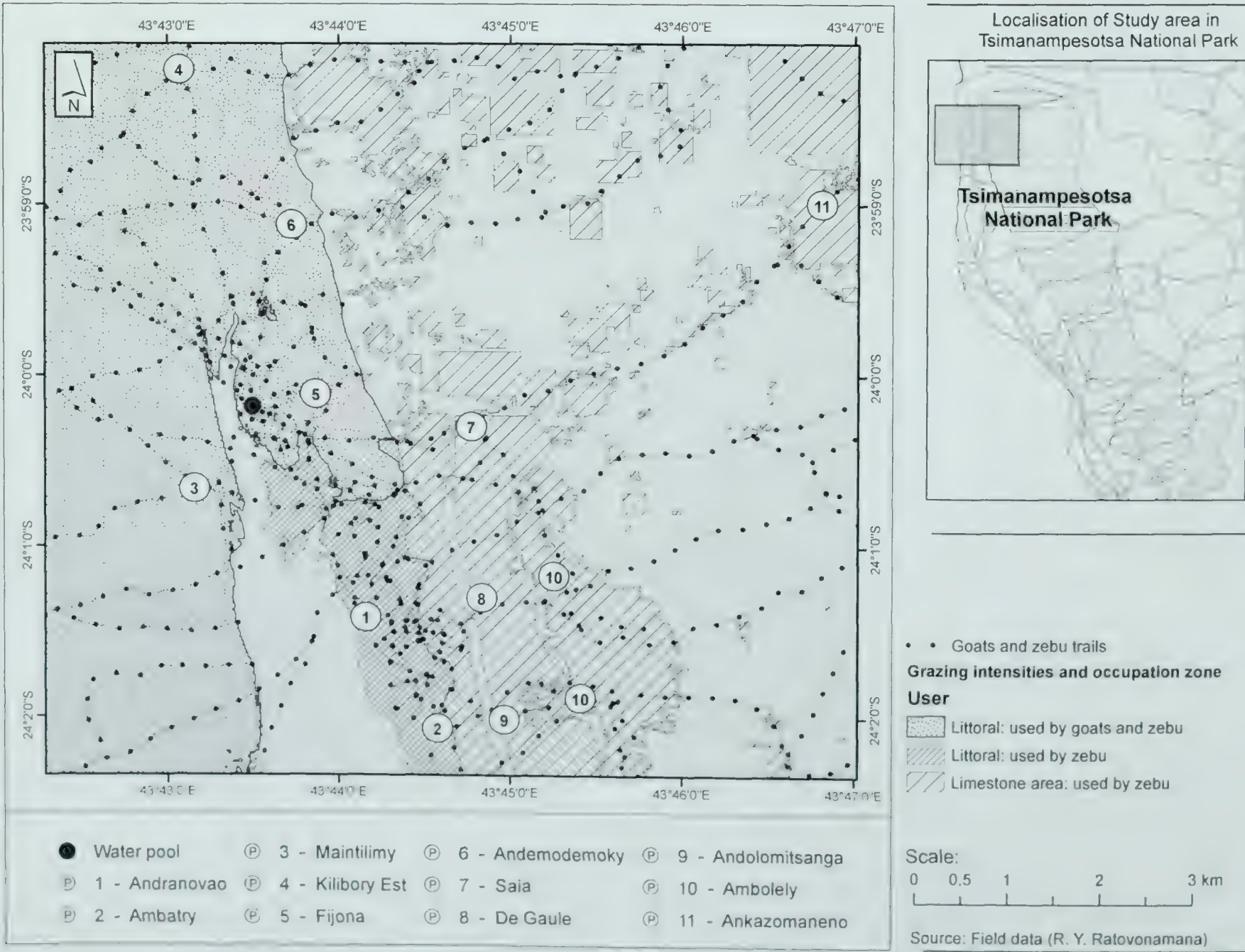


Figure 4 – Study sites in areas of different grazing intensities as described in table 1.

sequently, all edible parts (leaves and twigs to a diameter of 3 mm) were collected from the individual plant, dried and weighted. For each species, the dry biomass of edible parts was regressed against the crown volume with a linear regression that describes the allometric relationship between crown volume and food for livestock (Gregoire et al. 1995; electronic appendix 3). For the estimation of herbaceous biomass, all herbaceous plants were cut within the 1 m² subplots, dried and weighted. Available food biomass was summed for the different woody and herbaceous species and extrapolated to kg/ha.

Livestock stocking rates and ranging patterns

Assessment of the stocking rates and the habitat utilization by livestock is difficult as the number of livestock owned by a person is an economic (and thus tax) issue. The number of cattle and goats has been obtained from the official administration of the Commune of Beheloke. Analyses of habitat utilization patterns are hindered by the fact that livestock are not supposed to use the national park, while goats and cattle actually do use it. Therefore, the spatio-temporal patterns of grazing are based primarily on information provided by our long-term assistants from local villages based on their own experience and interviews.

Grazing pressure and carrying capacity

The determination of the carrying capacity requires knowledge about plant biomass production, consumption rate per unit livestock per day and the stocking rate per unit time.

One livestock unit (head of cattle under tropical conditions) is defined as an animal of 250 kg body mass (Unité de Bétail Tropical: UBT). Its consumption is defined as 6.25 kg of dry plant biomass per day (Consommation Journalière; Boudet 1975). One UBT is equivalent to one zebu or twelve goats. The grazing pressure was determined by comparison of the biomass production of the most important plant species and the food requirement of livestock.

Statistical analysis

Measurements of plant and vegetation characteristics were averaged per 15 × 15 m² plot. The individual plots served as unit for subsequent analyses. Data were tested for deviation from normality. Data deviating from normality were analyzed with non-parametric tests. All other variables were analyzed with parametric tests followed by Tukey’s Honest Significant Difference test for multiple comparisons. All tests were performed with the statistical package SPSS Base for Windows 13.0. Differences were considered significant at p ≤ 0.05.

RESULTS

Plant species and vegetation types within the study area

In the 66 plots of 15 × 15 m², we recorded 189 plant species from 56 different plant families with 126 plant species in the dry forest on sandy soil (littoral zone), 127 species on ferruginous soil (red sand), and 78 species in the xerophytic

Table 2 – Number of 15 × 15 m² plots, plant families, species and life forms in the major habitat types.

T: tree; S: shrub; L: liana; H: herb; P: parasite.

	Littoral	Limestone	Red sand
Number of 15 ×15 m ² plots	38	9	19
Families	46	33	44
Species			
Life forms			
T	24	15	26
S	54	43	60
L	17	8	18
H	30	12	23
P	1	0	0
Total	126	78	127

bush on limestone (table 2). The different numbers of species and families in the different formations cannot be compared directly due to the different number of plots per formation. The most important families are Fabaceae (29 species), Malvaceae (thirteen species), Apocynaceae and Euphorbiaceae (twelve species), Poaceae (ten species), Acanthaceae (nine species), Burseraceae (eight species) and Brassicaceae (six species). The different plant species, their growth forms, mean abundance per plot and their index of relative importance in the different zones are shown in the electronic appendix 1.

Livestock distribution

Goats and zebus occupied different proportions of the different vegetation types (table 3). Goats use only the littoral throughout the year. The animals leave the village every morning to graze in the littoral forest, especially those that are located around water points. Zebus also use the littoral forest, but only at the end of wet and the beginning of the dry season. Large parts of the spiny bush on the limestone massif

Table 3 – Surface (ha) of different vegetation types in the study area and the area used by goats and zebu during the wet and the dry season.

Vegetation types	Study area	Goats	Zebus
Dry forest in the littoral	601	472	596
Degraded dry forest in the littoral	1356	1288	1356
Herbaceous formations in the littoral	905	656	749
Dry forest on ferruginous soil	359	0	359
Xerophytic bush on limestone	434	0	55
Degraded xerophytic bush on limestone	3726	0	835
Bare soil and water	162	0	0
Herbaceous wetland formations	48	0	0
Total	7591	2416	3950

Table 4 – Effects of grazing on plant species numbers and different life forms in plots subject to different grazing pressure (GP, as defined in table 1).

N: number of 15 × 15 m² plots. Values are means ± standard deviations. Asterisks indicate significance levels according to Kruskal-Wallis analysis of variance: * p ≤ 0.05; ** p ≤ 0.01; *** p ≤ 0.001. Different letters indicate differences according to post-hoc tests.

Zone	N	Total number of species	Herb	Liana	Shrub	Tree
Littoral						
GP 1	4	47 ± 14 ^a	6 ± 2	3 ± 2	22 ± 7 ^a	15 ± 4 ^a
GP 2	8	23 ± 5 ^b	7 ± 3	3 ± 2	7 ± 4 ^b	5 ± 2 ^b
GP 4	26	20 ± 6 ^b	8 ± 2	2 ± 1	8 ± 3 ^b	3 ± 2 ^b
Chi-Square		11.78**	3.52	4.26	10.77**	16.51***
Limestone						
GP 1	5	33 ± 5	4 ± 1	4 ± 1	20 ± 3	6 ± 1
GP 2	2	23 ± 1	3 ± 1	2 ± 0	14 ± 1	5 ± 1
GP 3	2	28 ± 11	5 ± 1	3 ± 1	18 ± 7	3 ± 1
Chi-Square		2.96	1.54	2.82	2.90	5.83
Red sand						
GP 1	6	45 ± 7 ^a	3 ± 1	7 ± 2 ^a	21 ± 4 ^a	15 ± 2 ^a
GP 2	4	35 ± 4 ^b	3 ± 0	6 ± 1 ^a	15 ± 2 ^b	12 ± 2 ^a
GP 3	9	19 ± 3 ^c	4 ± 4	2 ± 2 ^b	7 ± 3 ^c	4 ± 4 ^b
Chi-Square		15.16***	1.65	11.72**	15.48***	14.51***

and dry forest on ferruginous soil (16% of the study area) are not used by zebus regularly (table 3, figs 1 & 4).

At the end of the dry season / beginning of the rainy season (November–December) the zebus west of Tsimanampesotsa NP are brought to the eastern part of the limestone massif to the region of Itomboina where extensive grasslands provide good pasture. At the end of the wet season (March), zebus cross the limestone plateau from east to west on a traditional track of transhumance in the northern part of Tsimanampesotsa NP. Initially, they remain on the coastal plain, but start moving into the national park as food abundance declines on the coastal plain during the dry season (figs 1 & 4).

Effects of grazing on the floristic composition and plant life forms

Plant species diversity changes with different grazing pressure and topographic position (table 4). In the littoral and on red sand, the mean number of plant species decreases significantly with increasing grazing pressure. On limestone, the species richness between sites with different grazing pressure did not differ significantly. The representation of different life forms did not differ under different grazing pressure in any of the habitats. An analysis of community similarity based on Spearman correlations between the occurrences of different plant species indicates that plant species composition is related more to the vegetation formation than to degradation (fig. 5).

In the littoral, the plots with low pressure (GP 1) are dominated by higher plant individuals (height > 50 cm) than the plots with medium (GP 2) and high (GP > 3) grazing pressure (fig. 6). In the limestone area, no significant differences were observed. On red sand, the communities are characterized by plants with heights below 25 cm, with a dominance of herbaceous species and rarity of woody plant in the 100–150 cm height class.

Indicator species

Electronic appendix 2 shows the most important plant species (defined by high values of relative importance) in relation to grazing pressure in the different vegetation types. The littoral plots with high grazing intensities (GP 3 and 4) were dominated by *Aerva javanica* (Amaranthaceae), *Setaria pumila* (Poaceae) and *Solanum hippophaeoides* (Solanaceae). These three species were absent in the plots not used by livestock. Some shrubs were more abundant in grazed than in ungrazed plots. These are *Acacia royumae*, *Alantsilodendron alluaudianum*, *Chadsia grevei*, *Mimosa delicatula* (Fabaceae) and *Rhigozum madagascariense* (Bignoniaceae). On limestone, the plots not used by zebu during the dry season, were dominated by *Panicum mahafalense* (Poaceae) and *Xerophyta tulearensis* (Velloziaceae). These two species constitute the main food source for cattle at the onset and during the dry season. On red sand *Aerva javanica* (Amaranthaceae), *Jatropha mahafaliensis* (Euphorbiaceae), *Uncarina stellulifera* (Pedaliaceae), *Alantsilodendron alluaudianum* (Fabaceae) and *Cucurbita* sp. (Cucurbitaceae) were more abundant in

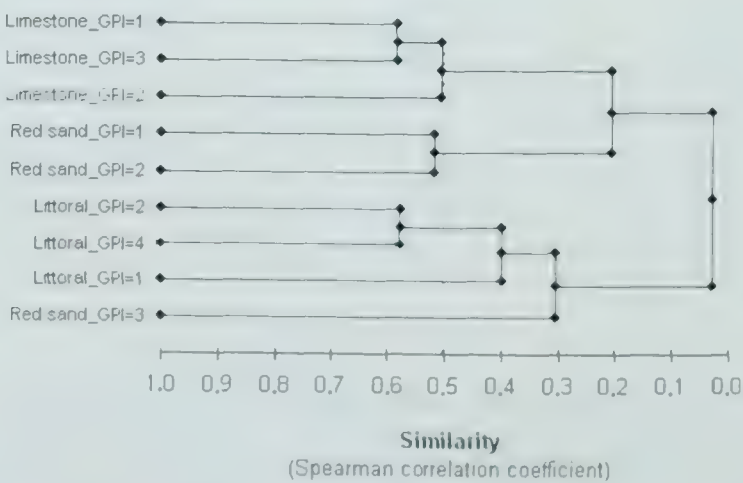


Figure 5 – Similarity of the floristic composition of plots in different categories of grazing pressure in the different zones.

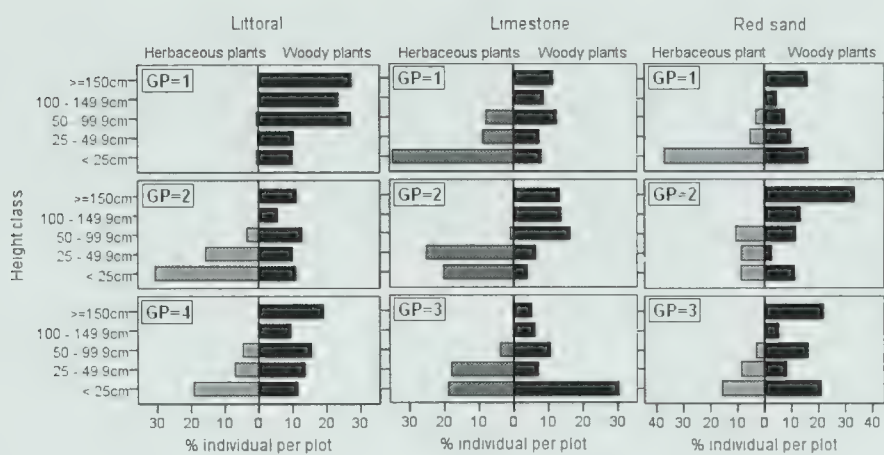


Figure 6 – Vegetation structure under different grazing pressure. Grazing pressure as described in table 1.

plots with high grazing pressure (GP 3) than in plots with low grazing pressure (GP 1) (electronic appendix 2).

Plant biomass

Table 5 shows the average biomass (dry plant material: DPM) of the most important food species in the study area. During the wet season (January–April) livestock used mainly the littoral. At this time of the year the most important food plants were: *Aerva javanica* (19.5–258.3 kg DPM/ha), *Boerhavia diffusa* (4.8–206.4 kg DPM/ha), *Dactyloctenium capitatum* (4.8–6.3 kg DPM/ha), *Indigofera diversifolia* (13.8 kg DPM/ha), *Panicum pseudovoeltzkowii* (37.8–75.6 kg DPM/

ha), *Panicum subalbidum* (176 kg DPM/ha), *Panicum maximum* (28.1 kg DPM/ha), *Tribulus cistoides* (50–365.2 kg DPM/ha), ‘*Tirinkitroky*’ (20–300 kg DPM/ha). The highest roughage biomass was recorded in April, at the end of the wet season (607 kg DPM/ha). The minimum was measured in February with 138.6 kg DPM/ha. The species *Tribulus cistoides*, *Panicum pseudovoeltzkowii*, and *Aerva javanica* were the most important food species at this time of the year. The average biomass available from these plant species per ha and their monthly changes are listed in table 5.

At the beginning of the dry season zebu started moving into the limestone area. During this time, roughage availability was still high due to the shift from herbs to the annual growth of trees and regenerating plants. *Indigofera peltieri* (1.5 kg DPM/ha), *Commiphora lamii* (4.1–6.8 kg DPM/ha), *C. marchandii* (263 kg DPM/ha), and *Plumbago aphylla* (3.38 kg DPM/ha) were the most important species for the littoral zone. Apart from these widely distributed species there were some highly productive patches of *Setaria pimula* (260 kg DPM/ha). *Xerophyta tuleariensis* (28.4 kg DPM/ha) and *Panicum mahafaliense* (232 kg DPM/ha) were most important in the limestone area.

During the dry season most woody plants lose their leaves and herbs disappear. In this season cattle were frequently found in the Tsimanampesotsa NP. Their staple food consisted almost exclusively of *Xerophyta tuleariensis* (55.5 kg DPM/ha), *Mollugo decandra* (6.1 kg DPM/ha), and *Gyrocarpus americanus* (15.4 kg DPM/ha) (table 5).

Table 5 – Average biomass of roughage per month of the most important food plant species during different times of the year. Values are kg of dry plant material per ha. Biomass was measured for the areas used by livestock in the different months. *Setaria pimula* had not been recorded in the standardized plots due to its patchy distribution, but represents an important fodder plant.

		Littoral				Littoral and limestone	Limestone and red sand
		Wet season				Onset of the dry season	Dry season
Month of roughage biomass estimates		Jan.	Feb.	Mar.	Apr.	May–Jun.	Jul.–Dec.
Species	Family						
<i>Panicum pseudovoeltzkowii</i>	Poaceae	75.6	37.8	34.1	-	-	-
<i>Aerva javanica</i>	Amaranthaceae	258	50.4	19.5	-	-	-
<i>Dactyloctenium capitatum</i>	Poaceae	-	6.3	4.8	-	-	-
<i>Boerhavia diffusa</i>	Nyctiginaceae	-	12.6	4.8	206.0	-	-
<i>Tribulus cistoides</i>	Zygophyllaceae	-	31.5	230.0	176.0	-	-
Indetermined (‘ <i>Tirinkitroky</i> ’)	Nyctiginaceae	-	-	12.9	189.0	-	-
<i>Indigofera diversifolia</i>	Fabaceae	-	-	13.8	-	-	-
<i>Panicum subalbidum</i>	Poaceae	-	-	-	17.6	-	-
<i>Panicum maximum</i>	Poaceae	-	-	-	28.1	-	-
<i>Panicum mahafaliense</i>	Poaceae	-	-	-	-	232.4	-
<i>Indigofera peltieri</i>	Fabaceae	-	-	-	-	1.5	-
<i>Commiphora lamii</i>	Burseraceae	-	-	-	-	6.8	4.1
<i>Commiphora marchandii</i>	Burseraceae	-	-	-	-	263.6	5.2
<i>Plumbago aphylla</i>	Plumbaginaceae	-	-	-	-	3.4	0.9
<i>Xerophyta tulearensis</i>	Velloziaceae	-	-	-	-	28.4	55.5
<i>Mollugo decandra</i>	Aizoaceae	-	-	-	-	-	6.1
<i>Gyrocarpus americanus</i>	Hernandiaceae	-	-	-	-	-	15.4
Total Biomass		333.9	138.6	319.9	617.5	536.1	87.2

Table 6 Available biomass of roughage and estimates of food requirements of goats and zebu in different zones used at different times of the year.

Wet season: January-March; end of the wet season: April; onset of the dry season: May-June; dry season: July-December.

	Wet season	End of wet season	Onset of dry season	Dry season
Livestock units: goats	574.75	574.75	574.75	574.75
Livestock units: zebu	-	4434	4434	4434
Livestock units per ha of littoral: goats	0.238	0.238	0.238	0.238
Livestock units per ha of littoral: zebu	-	1.642	-	-
Livestock units per ha of littoral and limestone: zebu	-	-	1.122	1.122
Food requirements per unit livestock (goats) per month occupying one ha	44.6 kg	44.6 kg	44.6 kg	44.6 kg
Food requirements per unit livestock (zebu) per month occupying one ha	-	307.9 kg	210.4 kg	210.4 kg
Total food requirements of livestock / ha	44.6 kg	352.5 kg	255 kg	255 kg
Available biomass of roughage (kg of dry plant material / ha)	264 kg	617.5 kg	536.1 kg	≤ 87.2 kg

Plant biomass available and total food requirements of livestock

The study area is stocked by the villages of Maromitilike, Efoetse, Marofijery and Ankilibory. According to official sources, their number of livestock was equivalent to 5009 UBT (4434 zebus + (6897 goats / 12) = 4434 + 574.75 UBT; total of 5008.75 UBT). Table 6 summarizes a rough estimate of the carrying capacity of the area where people of the villages listed above herd their livestock. The estimates are based on the following assumptions:

1. Goats were limited to the littoral zone and range over 2416 ha (table 3).
2. Zebu used 2701 ha of the littoral zone at the end of the wet season and included another 1249 ha on the limestone and red sand after the onset of the dry season (table 3).
3. The number of animals was assumed to be constant throughout the year, thus not taking into account reproduction. This underestimates food requirements.
4. Since zebu moved into the limestone area at the end of the dry season due to reduced food availability in the littoral zone, we assumed that food availability in the littoral zone is as low, or even lower than food availability in the limestone area. For the estimate of the carrying capacities we assumed that the same quantity of roughage would be available in both areas during the dry season (87.2 kg/ha). This overestimates food availability in the littoral zone.
5. Food requirements per unit of livestock are set as 6.25 kg roughage per day. This amounts to 187.5 kg of roughage per month per unit of livestock.

During the wet season, livestock which does not participate in the seasonal migration uses mainly the littoral zone. Here, the total biomass increased until the end of the wet season and decreased gradually during the dry season (table 6). According to the comparison between plant biomass available and total food requirements of livestock, food availability exceeded the needs of livestock during the six months between the wet and the onset of dry season. In contrast, food requirements of the animals were higher than food availabil-

ity during the six dry months. At this time, livestock relied heavily on the fodder produced within Tsimanampesotsa NP.

DISCUSSION

Grazing is a widespread form of land use in arid and semi-arid region (Riginos & Hoffman 2003). It can modify the floristic composition, spatial structure and representation of life forms in plant communities either through direct impact or to altered species interactions (Tielbörger & Kadmon 2000, Pykälä 2004, Cipriotti & Aguiar 2005, Jacobo et al. 2006, Sankey 2007, Škornik et al. 2010). Our study showed that species richness and diversity were affected differently by different grazing intensities and in different vegetation formations. In the littoral and on red sand, the plant diversity decreased with grazing pressure. Plots that were not used contained more woody plant species than area used by livestock at the end of wet season and during the dry season. The change in woody plant species structure favors the growth forms of herbaceous, desirable as well as unpalatable species. This change was most pronounced in the littoral zone, i.e. the area that is used by goats year-round and by zebu during the dry season. In contrast, livestock grazing had no statistically significant effect on species composition, diversity or structure on limestone. It seems unlikely that grazing does not have any effect on the plant communities on limestone. But we simply could not measure any effect, either because grazing intensity is actually very low or regeneration is so slow that effects of unhindered regeneration are not measurable, not even after four years without grazing (our category GP 1).

The effect of grazing on plant community structure and plant diversity can be explained by the availability of herbs and grass in the pasture area (Škornik et al. 2010). In our study, the total fodder biomass increased until the end of the wet season. It decreased gradually during the dry season. The comparison between plant biomass available and total food requirements of livestock showed that the plant biomass available exceeded the food requirements of the animals which remain in the area until the onset of the dry

season. But during the dry season the food requirement of the livestock exceeded the plant biomass available. By then, cattle switch from grazing on herbs and grasses to browsing on woody plants that still have leaves. The utilization of woody forage depends on the animals that remain in the pasture area. Goats eat a significant proportion of leaves from woody plants year-round, while zebu browse mainly during the dry season when the herbaceous forage is not available (Grouzis & Sicot 1980, Maiga 1995). Thus, the decline of liana, shrub and tree species with increasing grazing pressure indicate the dependence of livestock on woody species at the end of the wet season and during the dry season when the herbaceous plant species are not available. It should be kept in mind that data on livestock and ranging pattern are probably underestimated because the numbers obtained from the regional administration are unlikely to be complete. People at the villages are afraid that the neighbouring villages will know the number of their livestock. Furthermore, people use the national park as pasture. Since people recognize this as illegal, they are unwilling to reveal details about these activities and are hesitant to allow outside monitoring of their activities. In addition, livestock reproduction and thus seasonal changes in livestock numbers are not taken into account.

The increase of some species at high grazing intensities could be used as indication for grazing pressure. The increasing dominance of these plant species in grazed areas can be explained by two processes. First, some of the species are spread by livestock. These are *Aerva javanica* (Amaranthaceae), *Setaria pumila* (Poaceae), *Solanum hippophae-noides* (Solanaceae), *Alantsilodendron alluaudianum* (Fabaceae), *Erythrophysa aesculina* (Sapindaceae), *Poupartia minor* (Anacardiaceae), *Uncarina stellulifera* (Pedaliaceae) and *Cucurbita* sp. (Cucurbitaceae). Second, others species have a high regeneration capacity and are more resistant to cattle trampling. These are *Cedrelopsis grevei*, *Cedrelopsis gracilis* (Ptaeroxylaceae), *Rhigozum madagascariense*, *Stereospermum nematocarpon* (Bignoniaceae), *Chadsia grevei*, *Acacia royumae*, *Mimosa delicatula* (Fabaceae) and *Boscia longifolia* (Boraginaceae).

Apart from changes in species composition, we observed a relatively large difference in the representation of growth forms of plants across the different categories of grazing pressure. In grazed plots the percentage of plants in the lowest stratum increased in the littoral zone. This is opposite to the situation in many parts of Africa where grazing results in bush encroachment (Skarpe 1990, Moleele & Perkins 1998). In southwestern Madagascar herbaceous vegetation seems to increase with increasing grazing pressure. Yet, this is not due to an actual increase of herbaceous vegetation, but due to the reduction of trees and shrubs that are fed upon during the dry season when herbaceous plants are absent. Thus, the observed pattern is the outcome of the effect of grazing during the dry season when animals feed on woody vegetation because herbs are absent.

In summary, vegetation characteristics (species richness, species composition, plant life forms and vegetation structure) change with grazing pressure. The impact is most pronounced in the littoral and the red sand where vegetation cover is higher than on limestone. In the latter, grazing pressure seemed too low to have a measurable effect on plant

diversity and structure. Contrary to expectation, grazing did not result in bush encroachment as in many African countries, but favours herbs at the expense of woody vegetation, because herb biomass exceeds livestock food requirement during the wet season. During the dry season, herbs are no longer present according to their annual cycle. At this time of the year, livestock feeds extensively on woody vegetation that does not match the food requirements of the livestock at the present stocking rate and thus results in a decline of woody vegetation.

SUPPLEMENTARY MATERIAL

Supplementary data are available in pdf at the Supplementary Data Site of publications from the National Botanic Garden of Belgium (<http://www.nbgpublisher.be> > SBB50 > folder 612) and consist of (1) mean abundance of different plant species and their mean relative importance in the 15 × 15 m² plots of the different major habitat types in the study area; (2) relative importance of species under different grazing pressure; and (3) allometric calculation of edible plant biomass for various woody species.

ACKNOWLEDGEMENTS

The study was carried out under the collaboration between Madagascar National Parks (ex-ANGAP), the Departments of Animal Biology and Conservation, Department of Plant Biology and Ecology (Antananarivo University, Madagascar) and Department of Animal Ecology and Conservation (Hamburg University, Germany). We thank Mark Fenn, Jocelyn Rakotomalala and Domoina Rakotomalala (MNP Toliara, WWF Madagascar) Juliana Rasoma V. Rahantavololona, Jacques Solofomalala Rakotondranary and Peggy Giertz for their support. Special thanks go to our para-ecologists Mr. Louis Fisy and Mr. Mahita for their help in the field and for their communication skills with the local communities. The study was financed by WWF Sweden / WWF Madagascar with additional support from DFG/BMZ (Ga 342/15), VW Foundation, DAAD, WWF Germany and SuLaMa/BMBF. We highly appreciate the help and comments of Natacha Beau and two reviewers. The participation of R.Y. Ratovonamana at the AEFTAT congress was supported by the Hamburger Universitätsvermögen.

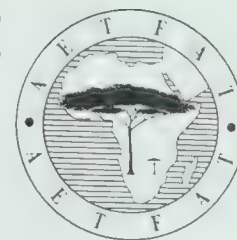
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Manuscript received 30 Nov. 2010; accepted in revised version 10 Dec. 2012.

Communicating Editor: Laurent Gautier.



Diversité floristique et caractères structuraux de quelques groupements végétaux de la Montagne d'Ambre (Nord de Madagascar)

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Study of the flora and vegetation of the Montagne d'Ambre (Northern Madagascar)

Background and aims – A study of the flora and vegetation of the Montagne d'Ambre was conducted to determine the floristic characteristics of this forest and to identify the different vegetation types present.

Material and methods – The study was done using 58 linear transects located at altitudes ranging from 890 m to 1430 m. Voucher specimens were prepared for identification and were deposited in national and international herbaria.

Key results – In total, 640 species and morpho-species in 249 genera and 99 families were identified. At the Montagne d'Ambre, floristic richness, diversity indices and canopy height decrease with altitude, while the percentage of cover of the lower strata of the vegetation increases.

Conclusion – This study highlights the effects of elevation and topographic position on floristic and structural characters of the forests above 800 m elevation on the Montagne d'Ambre.

Key words – Flora, vegetation, floristic richness, diversity, Montagne d'Ambre, Madagascar.

Contexte et objectif – Une étude de la flore et de la végétation de la Montagne d'Ambre a été réalisée afin de déterminer les caractéristiques floristiques de cette forêt et de connaître la typologie des formations végétales existantes.

Matériels et méthodes – L'approche a été réalisée à partir de 58 relevés linéaires situés à des altitudes comprises entre 890 m et 1430 m. Des échantillons de plantes ont été prélevés afin de les identifier dans les herbiers nationaux et internationaux.

Principaux résultats – Au total, 640 espèces et morpho-espèces réparties dans 249 genres et 99 familles ont été identifiées. A la Montagne d'Ambre, la richesse floristique, les indices de diversité et la hauteur de la canopée diminuent en fonction de l'altitude alors que le pourcentage de recouvrement des strates inférieures par la végétation augmente.

Conclusion – Cette étude a permis de mettre en évidence l'effet de l'altitude et de la topographie sur les caractéristiques floristiques et structurales des forêts dans les altitudes supérieures à 800 m de la Montagne d'Ambre.

INTRODUCTION

La Montagne d'Ambre est un massif de forêt dense humide sempervirente à l'extrême Nord de Madagascar (appendice électronique 1). Sa localisation isolée au sein d'une végétation sèche lui donne un caractère unique, lui conférant un intérêt majeur pour la recherche et la conservation. La forêt

dense humide de la Montagne d'Ambre a été rattachée au domaine du Centre, sous-domaine du Centre Nord, secteur de moyenne altitude, de la série à *Weinmannia* et *Tambourissa* par Humbert (1955). Malgré son statut de premier Parc National à Madagascar, créé en 1958, les connaissances scientifiques sur la flore et la végétation de cette montagne sont encore insuffisantes. En effet, les récoltes et expéditions ef-

fectuées jusqu’à l’heure actuelle (Rakotonandrasana & Roger 2005, Rakotoarimanana & Roger 2007) ne couvrent que les parties les plus accessibles du massif (le Nord et la partie Est) particulièrement à proximité de la station des Roussettes. Dans le but de vérifier l’hypothèse de l’influence des facteurs écologiques sur la diversité floristique et la structure forestière, cette étude a pour objectifs la description et la caractérisation de la flore et de la végétation de quelques groupements végétaux situés dans les zones les moins prospectées du massif (appendice électronique 2).

MATERIEL ET METHODE

Le travail est basé sur 58 relevés mixtes “ligne-surface” (Gautier et al. 1994), effectués dans les hautes altitudes du massif (de 890 à 1430 m) et dans six principaux sites de la Montagne d’Ambre (appendice électronique 3).

Le relevé linéaire est une méthode d’étude de la composition et de la structure de la végétation, permettant de déterminer la répartition verticale et le recouvrement des éléments végétaux. Dans une surface de végétation jugée homogène, une chevillement a été tirée sur une longueur de 100 m. Puis, un jalon de 8 m de haut a été déplacé tous les deux mètres le long de la ligne de 100 m (fig. 1). La hauteur de contact avec le jalon a été notée. Pour déterminer le nom scientifique, des échantillons de plantes (fertiles dans la mesure du possible) ont été prélevés, pressés et séchés à air chaud à l’aide d’un séchoir à gaz sur terrain. Les échantillons fertiles ont été déposés dans les herbiers nationaux (TEF) et internationaux Paris (P), Missouri (MO), Kew (K) et Wageningen (WAG). Les échantillons stériles ont été déterminés dans les herbiers nationaux TEF et TAN. Cette méthode a permis d’étudier la richesse floristique (effectif des familles, des genres et des espèces), la diversité floristique (indice de diversité de

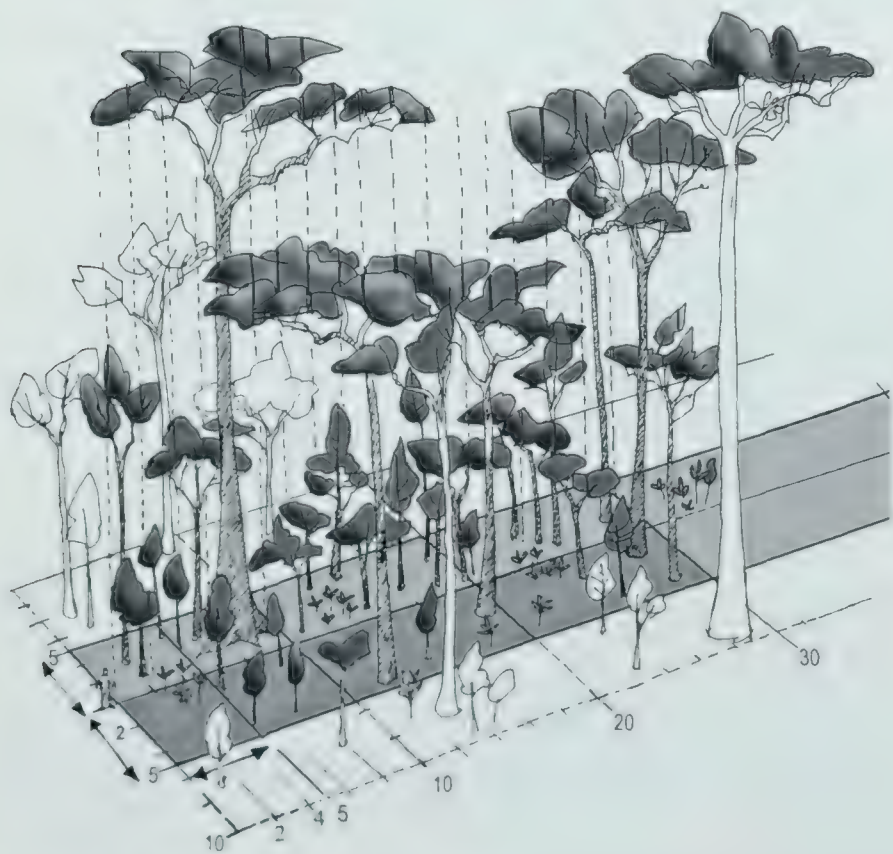


Figure 1 – Représentation schématique du relevé mixte ligne-surface d’après Cyrille Chatelain (Martin 2010).

Tableau 1 – Richesse floristique globale des forêts de la Montagne d’Ambre.

Taxons	Familles	Genres	Espèces
Angiospermes			
Dicotylédones	75	212	566
Monocotylédones	6	15	34
Gymnospermes	1	1	1
Ptéridophytes	17	21	39
Total	99	249	640

Shannon-Weaver, H’; indice de régularité, R) et le profil de la végétation. Le système de classification utilisé est l’APG III (Angiosperms Phylogeny Group 2009) pour les angiospermes et Smith et al. (2006) pour les ptéridophytes.

Le relevé de surface, composé par une parcelle de 0,1 ha, centrée sur la ligne médiane de chaque relevé linéaire a permis d’évaluer la densité du peuplement, la distribution des individus par classe de diamètre et la surface terrière. Les paramètres considérés sont le Diamètre à Hauteur de Poitrine (DHP) ≥ 10cm et la hauteur maximale (Hmax).

A chaque relevé effectué a été attribué un nom composé de l’initiale du massif suivie du numéro de relevé et du numéro de récolte (exemple: A01-001 où A désigne Ambre, 01, le numéro du relevé et 001, le numéro de l’échantillon). Les paramètres stationnels enregistrés ont été les coordonnées géographiques, l’altitude, la pente et la position topographique.

RESULTATS

Richesse floristique globale

Sur la base des 58 relevés linéaires, 640 espèces et morpho-espèces ont été identifiées. Ces espèces se répartissent dans 249 genres appartenant à 99 familles. Le tableau 1 résume la répartition des espèces recensées dans les différents rangs taxonomiques.

Richesse et diversité spécifiques des relevés linéaires

La diversité floristique des 58 relevés linéaires est présentée dans le tableau 2. Ce tableau est trié par ordre décroissant des valeurs de la diversité de Shannon-Weaver. De manière générale, l’analyse de ce tableau montre:

- une diminution du nombre d’espèces au fur et à mesure que l’altitude augmente: les relevés réalisés aux altitudes les plus basses (inférieur à 1000 m) de la Montagne d’Ambre sont les plus riches en espèces. Cela est illustré par le relevé A58 et A48, respectivement avec 86 et 83 espèces. De 1000 m à 1300 m d’altitude, la richesse spécifique diminue progressivement jusqu’à atteindre ses valeurs minimales au-delà de 1300 m. Enfin, vers 1380 m et 1430 m d’altitude, 32 et 34 espèces seulement ont été recensées (cas des relevés A01 et A06). Toutefois, quelques exceptions ont été constatées. Le relevé A02 réalisé à 1360 m présente encore un indice de diversité de Shannon Weaver élevé (3,304) probablement à cause

Tableau 2 – Diversité floristiques des relevés linéaires dans les altitudes supérieures de la Montagne d’Ambre.
Les données sont triées suivant l’indice de Shannon-Weaver décroissant.

Numéro relevé	Altitude (m)	Position topographique	Nombre de familles	Nombre de genres	Nombre d’espèces	Indice de diversité de Shannon-Weaver	Indice de Régularité
A58	995	Haut versant	42	69	86	4,058	0,943
A48	990	Haut versant	42	66	83	3,987	0,942
A14	1025	Mi versant	43	70	79	3,886	0,927
A52	970	Mi versant	35	60	77	3,884	0,937
A18	985	Mi versant	36	59	71	3,852	0,93
A32	1115	Mi versant	35	60	69	3,768	0,91
A43	1020	Bas versant	38	59	66	3,76	0,897
A33	1085	Mi versant	39	58	64	3,754	0,903
A50	920	Mi versant	33	57	69	3,737	0,899
A22	1150	Mi versant	34	62	69	3,715	0,904
A35	1040	Mi versant	34	54	61	3,71	0,922
A10	1180	Mi versant	36	55	66	3,699	0,886
A17	1060	Bas versant	39	60	71	3,691	0,894
A27	1060	Haut versant	33	59	67	3,674	0,93
A19	1035	Haut versant	36	59	63	3,67	0,904
A55	995	Mi versant	36	51	59	3,665	0,915
A45	990	Bas versant	39	57	65	3,654	0,896
A38	970	Mi versant	36	52	57	3,635	0,907
A53	1020	Mi versant	40	61	71	3,633	0,887
A49	980	Mi versant	35	60	75	3,597	0,868
A15	1275	Crête	34	47	52	3,582	0,92
A42	1025	Haut versant	33	45	55	3,58	0,902
A11	1250	Haut versant	41	58	71	3,555	0,876
A20	1000	Bas versant	38	61	67	3,552	0,864
A13	1010	Bas versant	38	56	61	3,546	0,897
A05	1210	Mi versant	35	50	55	3,538	0,9
A30	1082	Haut versant	31	51	57	3,519	0,899
A29	1123	Haut versant	28	46	54	3,511	0,928
A41	975	Bas versant	38	52	66	3,489	0,867
A37	1060	Mi versant	37	55	57	3,477	0,872
A56	930	MI versant	39	53	60	3,462	0,876
A51	890	Mi versant	33	56	72	3,455	0,874
A39	940	Bas versant	38	52	62	3,444	0,867
A44	965	Bas versant	42	61	64	3,442	0,834
A31	1040	Bas versant	32	49	52	3,426	0,911
A21	1175	Haut versant	33	52	56	3,418	0,903
A07	1340	Haut versant	31	43	46	3,399	0,909
A57	1020	Bas versant	33	51	61	3,381	0,848
A34	1140	Haut versant	33	44	50	3,379	0,864
A25	1065	Mi versant	27	48	54	3,368	0,89
A02	1360	Mi versant	35	43	48	3,304	0,863
A47	1030	Mi versant	33	53	62	3,297	0,834
A03	1270	Bas versant	31	50	56	3,292	0,846
A23	1050	Mi versant	28	44	48	3,281	0,878
A06	1430	Crête	27	33	34	3,272	0,906
A36	1080	Haut versant	37	50	54	3,27	0,84

Tableau 2 (suite) – Diversité floristiques des relevés linéaires dans les altitudes supérieures de la Montagne d’Ambre.

Numéro relevé	Altitude (m)	Position topographique	Nombre de familles	Nombre de genres	Nombre d’espèces	Indice de diversité de Shannon-Weaver	Indice de Régularité
A12	1280	Crête	33	50	50	3,269	0,892
A40	1010	Haut versant	32	40	48	3,265	0,863
A54	985	Mi versant	40	53	61	3,237	0,808
A46	900	Mi versant	29	44	53	3,136	0,819
A28	1140	Mi versant	28	49	56	3,07	0,793
A04	1250	Bas versant	22	37	38	3,056	0,859
A26	1012	Bas versant	25	38	44	3,004	0,838
A16	1288	Mi versant	26	34	37	2,984	0,846
A09	1190	Mi versant	33	44	49	2,971	0,768
A08	1330	Haut versant	24	32	35	2,821	0,814
A01	1380	Crête	22	32	32	2,693	0,8
A24	1150	Crête	22	33	36	2,689	0,798

d’un substrat moins sélectif sur un mi-versant exposé à l’ouest.

- une variation du nombre d’espèces en fonction de la topographie: à des altitudes similaires, les relevés sur crêtes sont moins riches par rapport aux relevés de versant et sur plateau.

Les valeurs de l’indice de diversité H’ confirment ces observations. En effet, les valeurs les plus faibles correspondent aux relevés effectués vers 1380m d’altitude (H’= 2,689). Quant à la régularité des espèces dans l’écosystème forestier en question, la valeur tourne autour de 0,8 et 0,9, ce qui montre une bonne équitabilité de répartition des espèces. Cependant, certains relevés (par exemple: A09) présentent des valeurs plus faibles, indiquant la dominance de quelques espèces. En effet, à certains endroits, la végétation est très ouverte et plus ou moins secondarisée. Certaines espèces secondaires y sont dominantes.

Structure de la végétation

Les 4 intervalles de hauteur les plus couramment utilisés à Madagascar (Messmer et al. 2002, Ranirison 2010) présentent des recouvrements caractéristiques au sein de la végétation. Chaque intervalle de hauteur est caractérisé par les espèces suivantes, par ordre de fréquence décroissante:

- l’intervalle de hauteur de 0 à 2 m est surtout représenté par des grandes fougères terrestres telles que *Christella distans* (Hook.) Holttum (Thelypteridaceae) et *Blotiella pubescens* (Kaulf.) R.M.Tryon (Dennstaedtiaceae), puis par *Impatiens* spp. (Balsaminaceae), *Begonia* sp. (Begoniaceae), *Asparagus simulans* Baker (Asparagaceae), *Streptocarpus* sp. (Gesneriaceae), *Cyperus* sp. (Cyperaceae), *Dianella ensifolia* (L.) DC. (Hemerocallidaceae) et *Brillantaisia madagascariensis* T.Anderson ex Lindau (Acanthaceae);
- l’intervalle de hauteur 2 à 4 m est dominé par *Psychotria polygrammata* Bremek. et *Pauridiantha paucinervis* (Hiern) Bremek. (Rubiaceae), *Clerodendrum pyrifolium* Baker (Verbenaceae) et *Dracaena* sp. (Convallariaceae);

- l’intervalle de hauteur 4 à 8 m est surtout représenté par *Tannodia grandiflora* Radcl.-Sm. (Euphorbiaceae), *Phyllarthron* sp. (Bignoniaceae), *Malleastrum* sp. (Meliaceae) et *Syzygium* sp. (Myrtaceae);
- l’intervalle de hauteur de 8 à 16 m est dominé par *Chrysophyllum boivinianum* Baehni (Sapotaceae), *Macaranga* sp. (Euphorbiaceae) et *Dombeya acerifolia* Baker (Sterculiaceae).

Le recouvrement est maximal dans l’intervalle de hauteur 0 à 2 m, puis diminue dans l’intervalle de hauteur 2 à 4 m pour augmenter progressivement vers les intervalles de hauteur supérieurs. Toutefois, la répartition verticale de la végétation présente une sensible variation suivant l’altitude et le niveau topographique. En effet, au fur et à mesure que l’altitude s’élève, la hauteur de la canopée diminue et le recouvrement des intervalles de hauteur inférieurs augmente (appendice électronique 4).

Six principales variantes structurales (fig. 2) ont été observées sur les 58 relevés:

- les formations très basses (hauteur moyenne = 4 m), à sous-bois très dense et dont le diamètre des troncs est très faible;
- les formations moins basses (hauteur moyenne = 10 m), à sous-bois dense et dont le diamètre des troncs est assez faible;
- les formations assez hautes (hauteur moyenne = 13 m), à sous-bois dense et à la voûte forestière assez régulière;
- les formations moyennement hautes (hauteur moyenne = 14 m), à sous-bois dense et à la voûte forestière d’une allure très irrégulière;
- les formations hautes (hauteur moyenne = 17 m), à sous-bois assez dense et dont le diamètre des troncs est élevé;
- les formations très hautes (hauteur moyenne = 19 m), à sous-bois assez clair et dont le diamètre des troncs est très élevé.

Suivant la position topographique, une nette variation a été observée. En effet, sur les crêtes, les individus de plus de 50 cm de DHP sont rares; en revanche, la densité des individus de plus faible diamètre est assez élevée. Sur les versants, les différences sont moins marquées. Toutefois, en bas de

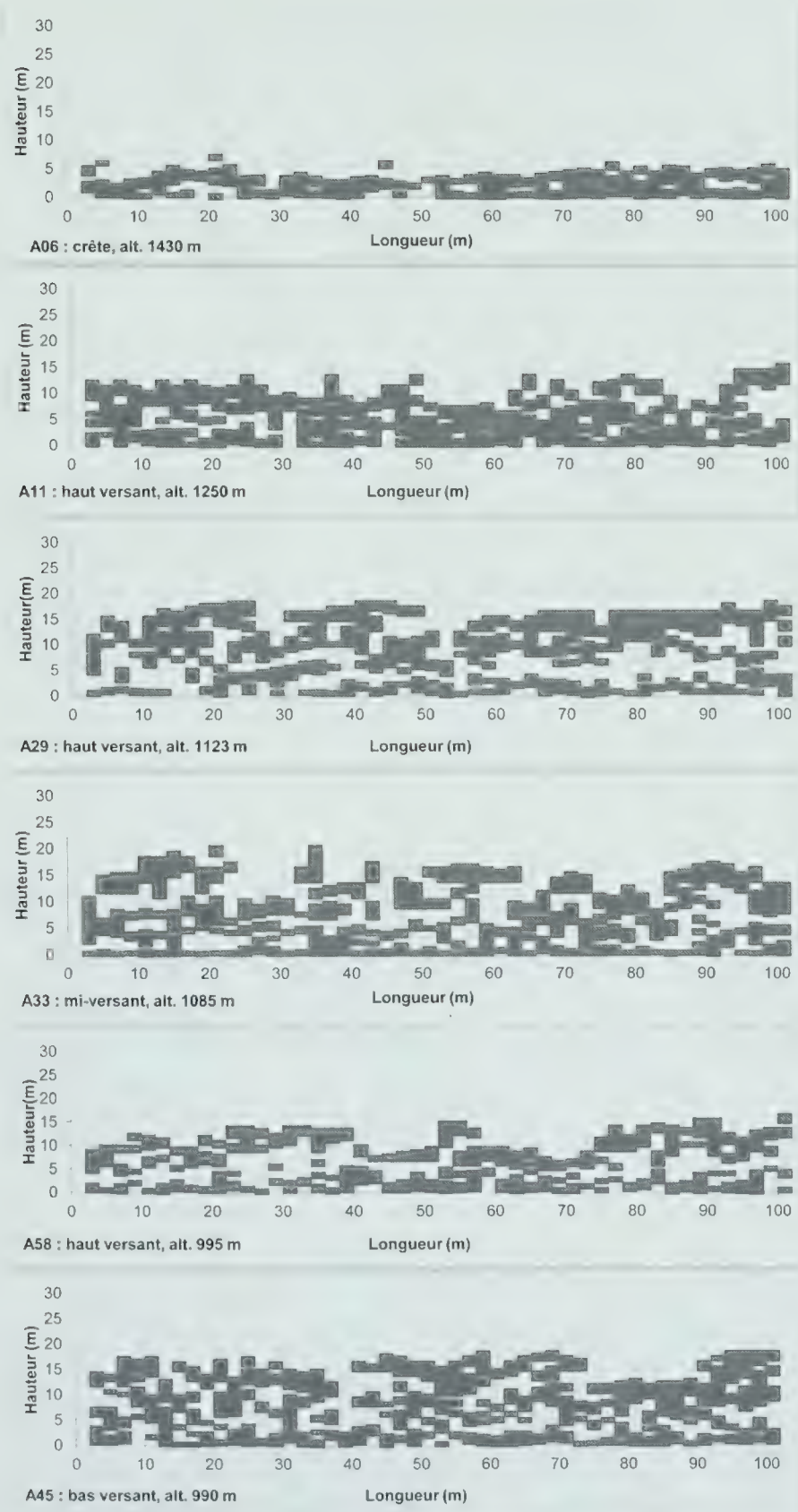


Figure 2 – Profils de végétation de six relevés représentatifs des variantes structurales. Les profils de végétation sont triés par ordre d'altitude décroissante.

versant, la densité des arbres de DHP 10–20 cm est peu élevée tandis que sur les mi-versants et les hauts versants, cette densité augmente. Il pourrait s'agir d'une organisation de la communauté pour l'exploitation des ressources. Les formations sont peu denses et les arbres développent un tronc considérablement plus large en bas de versant. Au fur et à mesure que le niveau topographique s'élève, la densité du peuplement augmente sensiblement et le DHP des individus diminue. Par ailleurs, l'absence de tronc large en haut de versant peut être due aux effets des cyclones qui rasent régulièrement les crêtes et les hauts versants. De manière générale, aucune nette variation n'a été décelée au niveau de la surface terrière sauf pour les relevés A25 et A06. La valeur particulièrement élevée de la surface terrière du peuplement du re-

levé A25 est liée au tempérament de certaines espèces telles que *Gyrostipula foveolata* (Capuron) J.-F. Leroy (Rubiaceae) dont le DHP peut atteindre 212 cm. Les crêtes très exposées ne permettent pas la persistance d'individus de plus de 50 cm de DHP, c'est le cas du relevé A06, réalisé à 1430 m d'altitude, où la surface terrière est très faible. L'exposition aux vents violents et à la température élevée constitue des facteurs limitant à l'installation de certaines espèces.

DISCUSSION

Diversité floristique

Concernant la relation entre les facteurs écologiques et la diversité floristique, une diminution de cette diversité a été remarquée avec l'augmentation de l'altitude à la Montagne d'Ambre (Ramandimbimanana 2009, Trigui 2010). Ce résultat semble être corrélé avec ceux obtenus dans plusieurs massifs montagneux de Madagascar comme à Manongarivo (Messmer et al. 2002), à Andohahela (Rakotomalaza & Messmer 1999), au Marojejy (Messmer et al. 2000) et à Daraina (Ranirison 2010). L'altitude est donc un des facteurs déterminant pour la richesse floristique au sein de la Montagne d'Ambre.

Comparaison floristique par rapport aux considérations phytogéographiques générales

La présence d'espèces de *Weinmannia* et *Tambourissa* dans la composition floristique des forêts de la Montagne d'Ambre correspond bien aux descriptions classiques de Perrier de la Bâthie (1921), de Humbert (1955) et de Humbert & Cours Darne (1965). De plus, les principales familles caractéristiques dans les moyennes altitudes comme Cunoniaceae, Monimiaceae et Araliaceae ont été observées. Certains taxons caractéristiques des forêts humides orientales malgaches sont en revanche absents dans les forêts de la Montagne d'Ambre. Parmi ces espèces figurent *Dilobeia thouarsii* Roem. & Schult., un taxon caractéristique des forêts de moyenne altitude (Koechlin et al. 1974). De même les familles des Sarcolaenaceae et Asteropeiaceae y sont absentes, pourtant, ces familles sont présentes à Manongarivo (Gautier 2002), au Marojejy (Messmer et al. 2000), ainsi qu'à Daraina (Ranirison 2010).

Comparaison floristique par rapport aux formations similaires du Nord de Madagascar

La Montagne d'Ambre est plus riche en taxons endémiques locaux (Trigui 2010) en comparaison avec deux massifs de la région nord de l'île: Manongarivo (Messmer et al. 2002) et Daraina (Ranirison 2010).

Structure de la végétation

La physionomie de certaines forêts de la Montagne d'Ambre retient l'attention à cause de certaines particularités (Razanajatovo 2009). Plusieurs constatations peuvent être formulées.

- Des espèces à larges contreforts comme *Canarium mada-gascariense* Engl. et *Chrysophyllum boivinianum* prédominant entre 1000 et 1200 m d'altitude. Pourtant, dans

la forêt orientale, les arbres à contreforts se rencontrent principalement dans les bas fonds, la présence contreforts augmentant sans doute leur stabilité. Le relief très accidenté du massif pourrait expliquer le développement des contreforts observés sur la plupart des arbres du massif, afin de leur garantir un meilleur équilibre.

- La découverte d'une faune actuelle dans les tufs basaltiques de l'extrême nord de Madagascar a permis de supposer que l'âge des dernières éruptions est subactuel (Decary 1922). Cependant, des études palynologiques ont permis de présumer que la Montagne d'Ambre était peuplée par les espèces végétales typiques de la forêt ombrophile de l'Est pendant les derniers 100 000 ans (Straka 1996). Ainsi, la forêt humide en place actuellement à la Montagne d'Ambre pourrait dériver de la forêt orientale dont le substrat a été surélevé suite aux activités tectoniques.
- La fréquence des ouvertures et des chablis dans de nombreux sites témoigne des exploitations antérieures entraînant la dominance des peuplements de *Harungana madagascariensis* Lam. ex Poir., habituellement observée dans les formations ouvertes, et des espèces secondaires comme *Dombeya acerifolia* et *Macaranga* sp. dans les strates arbustives et arborées. La situation isolée du massif qui l'expose directement aux vents et aux perturbations cycloniques accentuerait les effets de ces anciennes exploitations. Dans ces zones, de nombreuses espèces cicatricielles suffrutescentes telles *Strobilanthes madagascariensis* Baker et *Ionacanthus calcaratus* Benoist dominant la strate herbacée.
- Au-dessus de 900 m, les épiphytes, les lianes et les figuiers étrangleurs se rencontrent en abondance à différentes strates. Il s'agit d'*Asplenium nidus* L., de *Blechnum attenuatum* (Sw.) Mett, *Mendoncia cowanii* (S.Moore) Benoist, *Smilax anceps* Willd. et *Ficus* sp. Leur présence reflète une humidité atmosphérique élevée due à la présence de brouillard permanent. En outre, de nombreuses plantes herbacées ont une taille supérieure à 2 m. Les fougères arborescentes et les palmiers sont fréquents.

Les résultats de cette étude complètent les analyses structurales effectuées par Rakotonandrasana & Roger (2005), et Rakotoarimanana & Roger (2007) par l'étendue des zones prospectées et l'apport de techniques innovantes dans la prospection. Ces études antérieures étant réalisées une décennie auparavant (1997), les perspectives pourraient s'ouvrir aux analyses de l'évolution spatio-temporelle de ces formations végétales.

Comparaison de la végétation avec les formations similaires

Les formations étudiées à la Montagne d'Ambre dans le cadre de cette recherche présentent des caractères physiologiques, floristiques et biologiques similaires avec la forêt orientale de basse altitude: Masoala (Randrianjanahary 2004) et Mananara-Nord (Raharimalala 2000, Rakotoarivelo 1998).

CONCLUSION

Cette étude qui a porté sur la flore et la végétation de la Montagne d'Ambre a permis de mettre en évidence l'effet de l'altitude et de la position topographique sur les caractéristiques floristiques et structurales des forêts dans les altitudes supérieures à 800 m. Au total, 640 espèces réparties dans 249 genres et 99 familles ont été identifiées dans les relevés de végétation. Une diminution de la richesse floristique, de la diversité (indices de Shannon-Weaver et de régularité) ainsi que de la hauteur de la canopée en fonction de l'altitude et de la position topographique a été remarquée. De plus, la strate herbacée devient de plus en plus dense lorsque l'altitude augmente. Les résultats montrent que l'altitude et la position topographique sont à l'origine des particularités et de l'originalité floristiques des forêts au sein de la Montagne d'Ambre. La poursuite de cette étude vers les altitudes plus basses amènerait à considérer le gradient ombrothermique suivant l'altitude et l'effet de foehn dans les analyses. La pédologie pourrait également expliquer la diversité floristique et la structure forestière.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible au format pdf sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> > SBB50 > dossier 581) et comprend: (1) carte de localisation de la Montagne d'Ambre (vue en perspective); (2) tableau des coordonnées géographiques et de l'altitude des sites étudiés; (3) carte topographique du massif d'Ambre et localisation des sites d'études; (4) caractères structuraux et biométriques de relevés linéaires.

REMERCIEMENTS

Nous tenons à remercier le Département de Biologie et Ecologie Végétales (DBEV) et les Conservatoire et Jardin botaniques de la Ville de Genève (CJBG), où ces travaux ont été effectués. Nous avons également eu l'appui du Dr. C. Chatelain pour la gestion de la base de données du projet. Nous tenons à remercier également les différents spécialistes de taxons malgaches qui ont été consultés pour les déterminations. Le Ministère Français des Affaires étrangères par l'intermédiaire de l'initiative "Sud Expert Plantes, SEP 348" ainsi que le Fonds Marc Birkigt de la Société Académique de Genève ont soutenu financièrement ce projet.

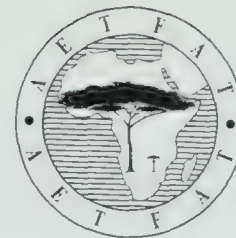
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Manuscript received 31 Oct. 2010; accepted in revised version 29 Mar. 2012.

Communicating Editor: Porter P. Lowry II.



Typologie de la synusie ligneuse de la forêt du Karthala, Archipel des Comores

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Typology of the woody synusium of the Karthala forest, Comoro Archipelago

Aim – We realised a phytoecological study in the Karthala forest. The objective was to define and characterise the main plants groups that could be used to adjust the biodiversity management and preservation programmes in the Comoro archipelago.

Methods – The phytoecological study was based on 78 vegetation relevés set up along fourteen transects arranged in an East-West direction following the altitudinal gradient. The data were subjected to multivariate analysis (FCA, FDA) to define the various groups. To characterise each group, we used Shannon diversity index, regularity index of Piélou and similarity index of Jacquard, as well as distribution of the woody species settlement.

Results – Natural forest area was discriminated from fields and cultural area. In the natural forest area, three groups were distinguished, according to the altitudinal gradient and the nature of the substrate: (a) forest of low and average altitude invaded by *Psidium cattleianum* var. *coriaceum*, (b) humid evergreen forest of high altitude with *Tambourissa comorensis* et *Weinmannia comorensis*, (c) forest of high altitude with volcanic lava flow characterised by *Rapanea comorensis* above which there is an ericoid moor with *Philippia comoriensis*. The study of the woody vegetation structural parameters showed a gradient of density that increases with the altitude, whereas the land area decreases. The same way, at higher altitudes the species richness and the regeneration potential of plants decrease.

Conclusion – The traditional methods of multivariate analysis allowed us to distinguish three different groups which differ from each other by their diversity and their structure, which are depending on presence and/or absence of human settlement, as well as on men's activities.

Key words – Characteristics, woody species settlement, floristic inventories, altitude, Indian Ocean, Comoros.

Objectif – Nous avons réalisé une étude phytoécologique dans la forêt du Karthala. L'objectif était de définir et de caractériser les principaux groupements végétaux pouvant être utilisés pour mieux orienter les programmes de gestion et de conservation de la biodiversité dans l'archipel des comores.

Méthodes – L'étude phytoécologique fut réalisée à partir de 78 relevés de végétation établis le long de quatorze transects disposés dans le sens Est-Ouest suivant le gradient altitudinal. Les données ont été soumises à des analyses multivariées (AFC, AFD) pour définir les différents groupes. L'indice de diversité de Shannon, l'indice de régularité de Pielou, l'indice de similarité de Jaccard, la structure du peuplement ligneux ont été utilisées pour caractériser chaque groupement identifié.

Résultats – La forêt naturelle et les champs ont été séparés. Dans la forêt naturelle nous avons par ailleurs distingué trois groupements repartis suivant le gradient altitudinal et la nature du substrat: (a) une forêt de basses et moyennes altitudes envahie par *Psidium cattleianum* var. *coriaceum* (b) une forêt humide sempervirente de hautes altitudes à *Tambourissa comorensis* et *Weinmannia comorensis* (c) une forêt des hautes altitudes inféodée aux coulées de lave volcanique caractérisée par *Rapanea comorensis* au dessus de laquelle se trouve une lande éricoidale à *Philippia comoriensis*. L'étude des paramètres structuraux de la végétation a révélé un gradient de densité, qui croît avec l'altitude tandis que la surface terrière diminue. De même en altitude, la richesse spécifique a diminué ainsi que le potentiel de régénération des arbres.

Conclusion – Les méthodes classiques d'analyses multivariées nous ont permis de distinguer quatre groupements qui diffèrent les uns des autres par leur diversité et leur structure, ces dernières étant tributaires de la présence/absence d'habitations et de l'action de l'homme.

INTRODUCTION

L'archipel des Comores est situé dans la partie nord du canal de Mozambique à mi-distance entre Madagascar et l'Afrique. Il provient d'un volcanisme océanique, et n'a jamais été en contact avec aucune masse continentale (Legris 1969).

La diversité de ses habitats et la richesse de sa flore et de sa végétation, comme pour tout autre île, résultent de la combinaison entre relief et topographie d'une part et d'un ensemble d'espèces végétales migrant de zones continentales les plus proches d'autre part (Pascal 1997).

Les origines de la flore de ses îles établies par Pascal et al. (2001) pour Mayotte, la plus vieille et la plus orientale et par Charahabil (2011) pour la Grande-Comore, la plus jeune et la plus occidentale de l'archipel ont mis en évidence la prédominance des espèces d'origines malgaches sur les éléments d'origine africaines.

Malheureusement la structure de la végétation dans cet archipel et particulièrement du Karthala, la plus grande forêt climacique de la grande île est très peu étudiée. Une classification des différents types de formations forestières des Comores a été établie sur la base d'inventaires peu exhaustifs basés sur l'ethnobotanique et la pharmacopée traditionnelle (Adjanohoun et al. 1982). Ainsi la végétation des Comores comprendrait des formations naturelles (forêts denses et humides, formation arbustive ou buissonnante, savane et mangrove), des formations anthropisées, des plantations d'arbres (*Eugenia aromatica*, *Artocarpus heterophilus*, *Mangifera indica*...) et des zones de champs.

Ducatillon & Loup (1985) ont étudié les espèces ligneuses dans le paysage forestier des Comores et ont confirmé l'existence de ces formations en précisant la structure duale de la végétation qui est composée d'une forêt de basses altitudes et d'une forêt humide de haute de hautes altitudes au dessus de laquelle on trouve une lande à Éricacées tout près du sommet du volcan.

Des travaux récents (Keith et al. 2006) basés sur des inventaires faunistiques et floristiques dans l'archipel ont indiqué qu'il existe deux types de végétation climaciques: les forêts caducifoliées de basses altitudes et les forêts denses humides de moyennes et hautes altitudes.

La destruction des écosystèmes insulaires tropicaux très fortement engagée n'épargne pas la végétation de ces îles de

l'archipel des Comores notamment sa composante ligneuse. Les populations exercent en effet de fortes pressions sur ces écosystèmes qui, associées à l'effet de la dégradation des conditions climatiques font reculer ces forêts. Selon Unep (2002), 74% des ménages comoriens utiliseraient le bois comme source principale d'énergie domestique. En outre, la pauvreté récurrente et la proximité des plantes entraînent de plus en plus un très grand recours aux plantes médicinales (Zainaba 2009).

Or à ce jour, les connaissances scientifiques nécessaires à la mise en place de programmes de gestion durable de la biodiversité dans cet archipel manquent cruellement.

Les études sur la végétation des Comores sont très rares pour ne pas dire inexistantes et les études sur la caractérisation de la flore reprennent le plus souvent la seule liste publiée jusqu'à nos jours par Voeltzkow (1917).

Cependant, un effort d'inventaire a débuté il y a une dizaine d'années dans le cadre d'un partenariat entre le Muséum de Paris et les centres de recherches aux Comores. Ainsi, quelques articles portant sur la taxonomie et la description de nouvelles espèces aux Comores ont été publiés: Labat & Du Puy (1997), Labat et al. (1999, 2000), Mouly (2007, 2009). L'ensemble de ces travaux ont montré que la flore ligneuse constitue l'essentiel du paysage des forêts de l'archipel et particulièrement de la forêt du Karthala. Une étude de la végétation basée uniquement sur cette composante ligneuse permettrait de décrire de manière assez suffisante l'organisation et la structuration de cette végétation. Dans cette étude, nous tentons de répondre à cette question à travers une typologie des formations ligneuses de la plus grande forêt climacique de l'île et de l'archipel des Comores. Les méthodes d'analyse multivariées largement utilisées en phytoécologie (Akpo et al. 1995, 2003, Diatta et al. 1998) sont utilisées pour définir ces unités de végétation. Les paramètres structuraux quantitatifs de la végétation et les indices de diversité (alpha et beta) seront utilisés pour caractériser les groupements définis.

METHODES D'ETUDES

Site d'étude

L'étude a été réalisée dans la forêt du Karthala située en Grande Comore, l'île la plus occidentale de l'archipel des Comores.

La superficie totale du site est estimée à 13000 ha dont 6300 ha correspondent à la forêt, 5000 ha à une lande d'Éricacées situées dans les étages altimontains proches du sommet du volcan. Le reste de la superficie couvre la caldeira (DNEF 2006).

Les sols sont perméables et peu altérés. Le climat est de type tropical humide sous l'influence de deux types de vents: les alizés du Sud-est qui entraînent la saison relativement sèche et fraîche de Mai à Octobre, et les moussons du Nord-ouest entraînant une saison de pluie, chaude et humide de Novembre à Avril.

Les pluviométries moyennes annuelles varient entre 1398 mm et 5888 mm et les températures sont de l'ordre de 27°C au niveau de la côte. Elles varient très peu avec l'altitude pour atteindre des minima de 0°C au sommet du Karthala avec une variation appréciable de l'humidité relative.

La collecte des données

La méthode des relevés de la végétation a été utilisée pour cette étude. L'échantillonnage est basé sur des transects (Gounot 1969, Charahabil et al. 2008). Pour mieux embrasser les limites phytogéographiques prédéfinies nous avons espacé les relevés de 100 à 200 m d'altitude sur chaque transect. Des relevés ont été effectués dans les champs situés dans les basses altitudes du fait qu'ils constituent dans certains endroits des fragments de forêts secondaires. Au total quatorze transects orientés suivant le gradient et totalisant 78 relevés ont été délimités. La surface de chaque relevé est de 100 m², équivalent à l'aire minimale de la zone définie par Campbell & Hammond (1989).

Une partie des espèces a été identifiée à l'aide de la flore de Madagascar et des Comores (Humbert & Leroy 1936–onwards), le reste étant identifié grâce à la base de données (<http://coldb.mnhn.fr/Consultation?catalogue=1>) des échantillons de l'herbier du Muséum d'Histoire Naturelle de Paris (P).

Une nomenclature binomiale a été utilisée pour distinguer les sols noirs forestiers de types hydromorphes des sols volcaniques sur les coulées de lave basaltique.

L'évaluation de la densité des espèces s'est effectuée par un comptage exhaustif des ligneux dont le DBH (Diameter at Breast Height: diamètre à hauteur de poitrine) est supérieur à 10 cm. Pour des espèces multicaules comme *Psidium cattleyanum* var. *coriaceum*, nous avons considéré toutes les tiges émergentes (pieds et rejets).

Traitement des données

Définition des groupements floristiques – Nos relevés ont été traités par la méthode d'analyse factorielle de correspondance (AFC) basée sur le principe de l'inertie, de la contribution et de la corrélation.

L'inertie permet de quantifier l'information contenue dans chaque axe. La contribution évalue le poids des individus ou des variables à la constitution d'un axe. La corrélation permet, quant à elle, de mesurer la qualité d'un point sur un axe ou sur le plan factoriel formé par deux axes. Pour évaluer la stabilité des groupes issus de l'AFC, nous avons utilisé la

méthode Disqual ou méthode de discrimination sur variables qualitatives (Saporta 1990). Elle consiste à réaliser une analyse factorielle discriminante (AFD) sur une matrice dont les variables qualitatives q sont remplacées par les coordonnées p sur les axes factoriels.

Floristique et structure des groupements – Les paramètres structuraux quantitatifs de la végétation (densité, surface terrière, régénération, richesse spécifique, hauteurs maximales des arbres) ont été utilisés pour caractériser les groupements.

L'indice de similarité de Jaccard (1901) a été utilisé pour comparer la diversité floristique entre les unités de végétation.

Pour comparer le niveau d'organisation des groupements définis, nous avons choisi d'utiliser l'équitabilité de Pielou, ou régularité, du fait que ces groupements diffèrent entre eux tant par leur effectif d'arbres que par la diversité floristique.

$$R = \frac{H'}{\log 2S}$$

(H' : indice de Shannon-Weaver ; S nombre d'espèces)

R varie entre 0 (régularité nulle) et 1 (régularité maximale). Théoriquement cette valeur maximale est atteinte lorsque toutes les espèces sont représentées par un même nombre d'arbres).

Pour la détermination des espèces indicatrices, nous avons utilisé la méthode IndVal, qui repose sur le caractère indicateur d'une espèce basé sur:

- sa spécificité qui évalue le degré de présence d'une espèce uniquement dans un seul groupe:

$$A_{ij} = N_{\text{individus}_{ij}} / N_{\text{individus}_i}$$

- sa fidélité qui exprime son degré de répartition à l'intérieur du même groupe:

$$B_{ij} = N_{\text{sites}_{ij}} / N_{\text{sites}_j}$$

L'Indval est la valeur indicatrice de l'espèce i dans le groupe de relevé j :

$$\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100$$

RESULTATS

Analyse globale

La matrice 78 relevés/95 espèces ligneuses a été soumise à une analyse factorielle de correspondance (fig. 1). La variance totale du tableau issue de cette analyse est de 8,09 dont 7,47% sont portés par le premier axe (F1), 5,8% par le second, 4,75% par le troisième et 4,1% par le quatrième. Le plan factoriel F1 et F2 apporte 13,27 % de la variabilité totale, pourcentage largement acceptable si l'on tient compte du nombre de relevés.

Les relevés et les espèces qui ont significativement contribué à la formation de l'axe F1 se distinguent dans l'extrémité positive de l'axe. Ce sont des relevés situés dans les basses altitudes et les faibles reliefs correspondant aux champs (R14, R66, R27, R1, R21, R22, R44, R2, R55, R66). Les espèces associées à ce groupe de relevés sont: *Buddleja indica*, *Fluggea virosa*, *Euclea mayottensis*, *Cocos nucifera*. Ce groupe s'oppose aux relevés des hautes et moyennes al-

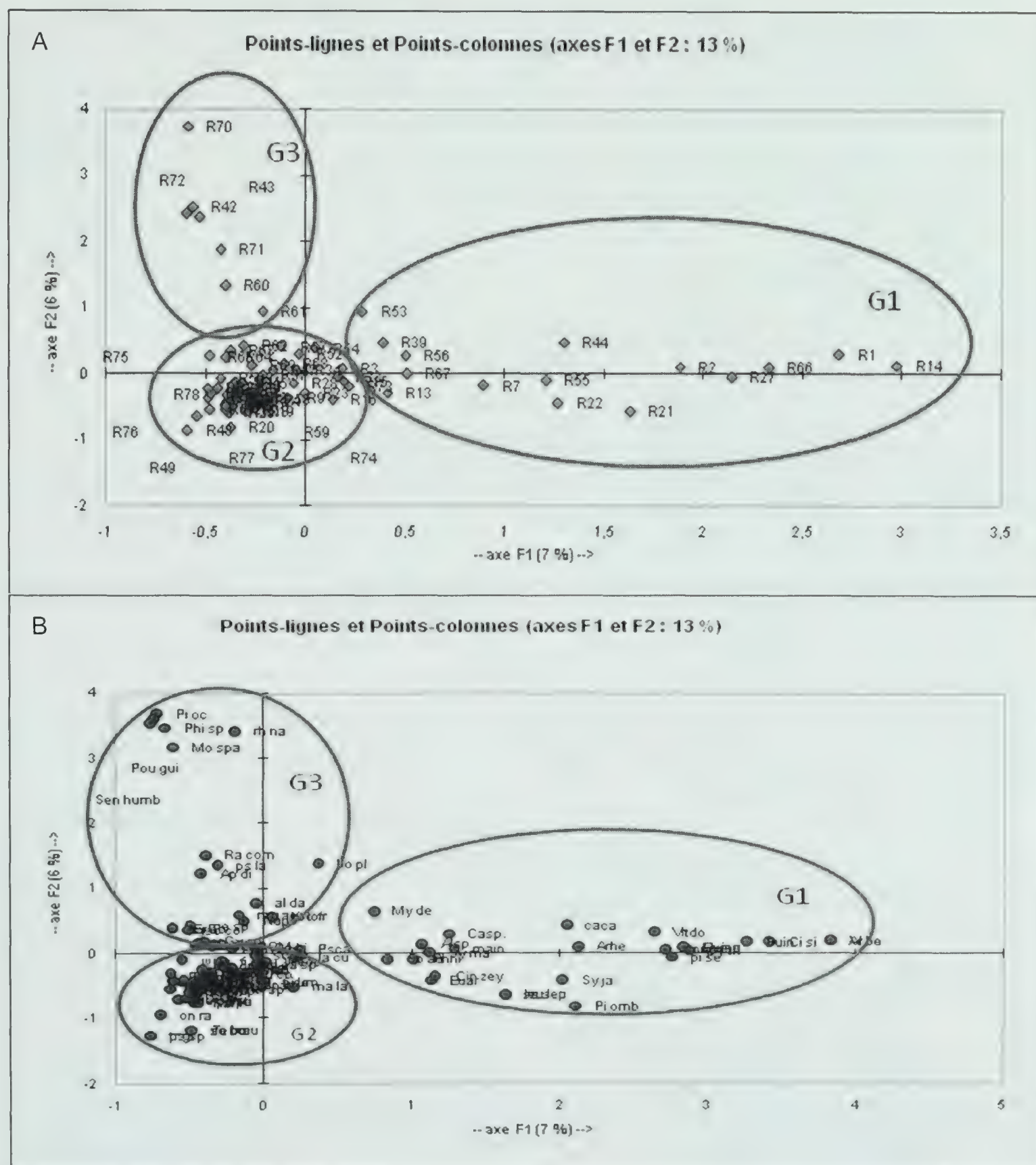


Figure 1 Analyse globale dans le plan des facteurs F1 et F2 de la matrice 78 relevés $\times$ 95 espèces: A, carte des relevés; B, carte des espèces.

titudes correspondant à la forêt naturelle. Les contributions relatives des relevés et des espèces à la formation de l'axe sont inférieures à la moyenne. Les espèces associées à cet ensemble sont: *Ocotea comoriensis*, *Weinmannia comorensis*, *Anthocleista grandiflora*, *Tambourissa comorensis*. Ce sont des espèces autochtones et endémiques du pays et du Karthala (fig. 1B).

C'est l'axe F2 qui permet de comprendre cet ensemble. En effet, on distingue à l'extrémité positive de cet axe, des relevés inféodés à des sols volcaniques sur les coulées de lave basaltique (R70, R71, R72, R43, R60, R6). Ces relevés se situent généralement dans les hautes altitudes près de la lande à Éricacées qui constitue la limite supérieure de la végétation. Dans cet ensemble de relevés on retrouve les espèces suivantes: *Philippia comoriensis*, *Rapanea comoren-*

sis, *Apodytes dimidiata*, *Senecio humblotii*, *Rhus natalensis*.
A l'extrémité négative de l'axe on trouve des relevés de hautes et moyennes altitudes sur un substrat humide dont le sol a généralement évolué en sol noir forestier.

L'analyse globale a permis d'identifier trois groupements (fig. 2A & B):

L'axe F1 a distingué nettement les champs (G1) et la forêt naturelle (ensemble G2 et G3) et l'axe F2 a permis de distinguer dans la forêt naturelle, les groupements G2 correspondant à la forêt humide de hautes et moyennes altitudes dont le substrat est humide sur un sol noir forestier et le groupement G3 correspondant aux forêts de hautes altitudes sur les coulées de lave de type basaltique.

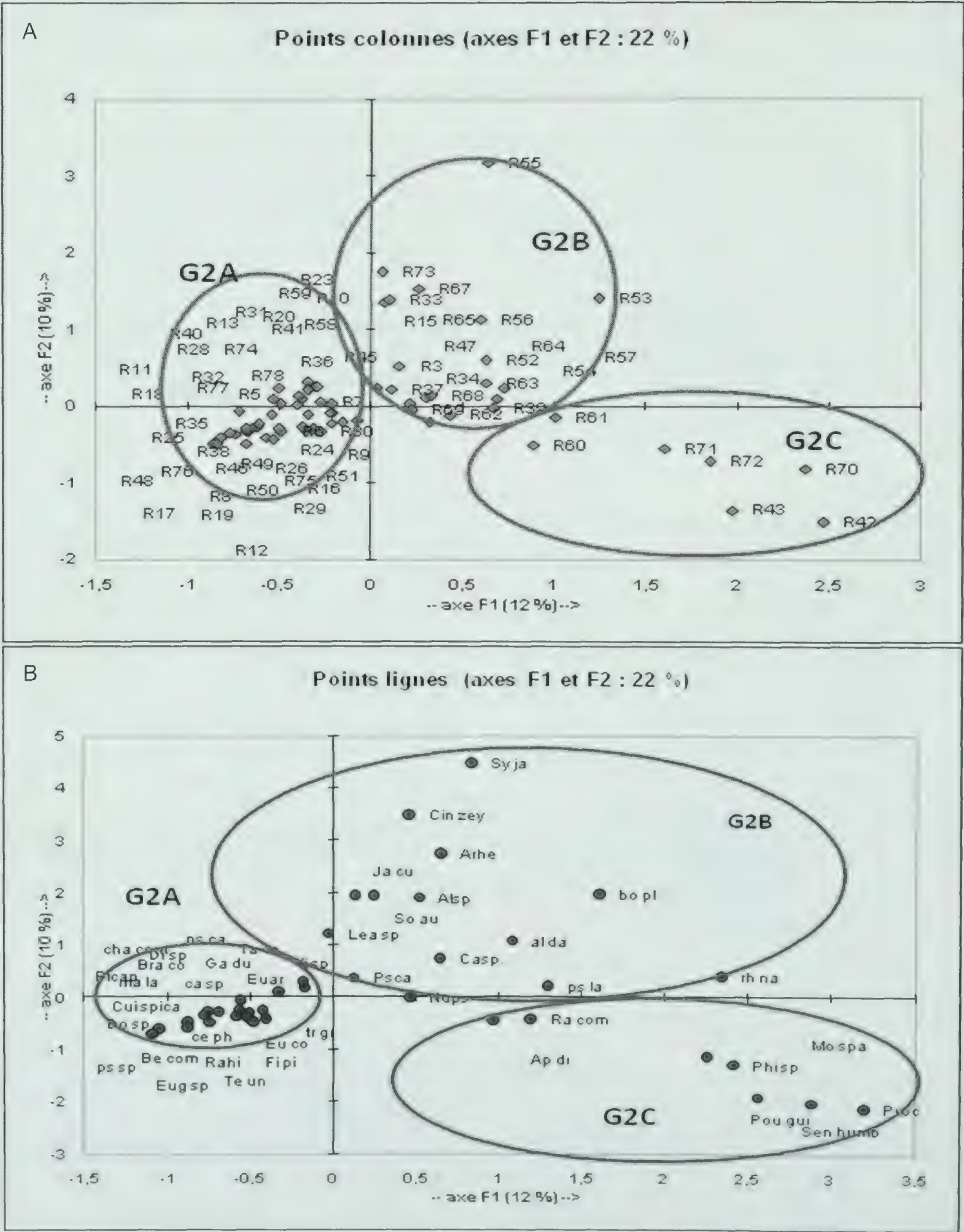


Figure 2 – Analyse partielle sur le plan F1 et F2 de la matrice 70 relevés/43 espèces: A, carte des relevés; B, carte des espèces.

Pour évaluer la stabilité des groupements ainsi définis nous avons réalisé une Analyse factorielle Discriminante (AFD).

L'AFD a donc été réalisée sur quatre variables qualitatives (coordonnées sur les axes factoriels F1, F2, F3, F4). L'inertie totale est de 0,694 bits, l'axe F1 en contient 0,693 (variance = 99,920%). Cet axe est largement suffisant pour

séparer les groupes dans un plan à deux dimensions. Les résultats de l'analyse sont présentés dans le tableau 1.

L'analyse du tableau d'appartenance indique que 78,21% des relevés sont bien classés.

Le groupe G1 (champs) paraît peu stable. Les relevés R3, R7, R13, R15, R33, R39, R55, R56, R67, R53 seraient mal classés, car ils sont affectés au groupe G2. Huit relevés seule-

Tableau 1 – Analyse factorielle discriminante: tableau d'appartenance des différents groupes.

	G1	G2	G3	Somme
G1	8	10	0	18
	10,26%	12,82%	0,00%	23,08%
G2	0	53	0	53
	0,00%	67,95%	0,00%	67,95%
G3	0	7	0	7
	0,00%	8,97%	0,00%	8,97%
Somme	8	70	0	78
	10,26%	89,74%	0,00%	100,00%

ment sont restés stables (R1, R2, R14, R21, R22, R27, R44, R66). Ils constituent réellement le groupement des champs.

Le groupe G2 est le groupe le mieux classé, tous ses relevés sont stables. Il renferme 67,95% des relevés bien classés. Le groupe G3 qui correspond au relevé inféodé aux coulées de lave basaltiques est le plus instable, tous les relevés du groupe sont versés dans le groupe G2. Vu le taux d'erreur, nous avons isolé le groupement des champs et réuni les relevés mal classés en un seul groupe (forêt proprement dite) que nous avons soumis à une seconde analyse.

Analyse partielle (typologie de la forêt naturelle)

Une seconde AFC a donc été appliquée sur une matrice 70 relevés/43 espèces. (fig. 2). Nous avons retiré de l'analyse les espèces à contribution nulles ou insignifiantes afin d'atténuer l'effet mosaïque dû à la prédominance des ces espèces.

Les quatre premiers axes rendent compte de 34,43% de la variabilité totale. Le plan factoriel F1 et F2 en extrait 21,68%.

En abscisses négatives de l'axe F1, on retrouve les relevés associées aux zones humides des hautes altitudes (> 1100 m²). Les précipitations sont abondantes et le sol a évolué en sol noir forestier de type hydromorphe. On y trouve des espèces telles que *Cussonia spicata*, *Ravenea hildebrandtii* et *Piper capense*.

En abscisses positives, on retrouve un autre groupe de relevé que l'axe F2 sépare en deux sous groupes:

En ordonnées positives se distinguent les relevés des forêts basses (altitude inférieure à 1100 m). Les espèces associées à ce groupement sont: *Albizzia glabereima*, *Syzygium jambos*, *Cinnamomum zeylanicum*, *Psidium cattleyanum*, *Leea guineensis*. Le substrat est aussi un sol noir forestier de type hydromorphe.

En ordonnées négatives, on se retrouve dans les très hautes altitudes près de la lande à éricacées. Le substrat est volcanique sur une coulée de lave basaltique fait que l'eau ruisselle et devient peu disponible pour les plantes. Les espèces qui y sont inféodées développent des stratégies d'adaptation à ces conditions particulières:

- feuilles charnues (*Rapanea comorensis*, *Apodytes dimidiata*)
- feuilles réduites (*Philippia comoriensis*, *Senecio humblotii*, *Pouzolzia guineensis*, *Morella spathulata*).

L'axe F1 constitue donc un gradient d'humidité décroissant et l'axe F2 constitue un gradient altitudinal décroissant couplée de l'effet du type de sol (volcanique ou non) sur la rétention de l'eau pour les plantes (fig. 2B).

L'analyse a donc permis d'individualiser trois groupes: G2A: forêt humide, G2B: forêt de basses altitudes et G2C, forêt de hautes altitudes sur les coulées de lave basaltiques

Caractérisation des unités de végétation ligneuses

Notion de fidélité, et de spécificité: les espèces indicatrices

– La fidélité d'une espèce est un caractère important dans l'étude des groupements végétaux. Les espèces "fidèles" marquent en effet leur préférence pour un milieu particulier soit par une grande abondance soit par une forte vitalité contrairement à d'autres groupements.

Les espèces ligneuses recensées dans l'ensemble des quatre unités de végétation peuvent être distinguées en deux groupes selon la fréquence de présence:

- le premier groupe est constitué des espèces communes ou indifférentes, on les rencontre dans les quatre unités de végétation. Ce sont des espèces très fréquentes. Il s'agit *Canthium* sp., *Eugenia comorensis*, *Nuxia pseudodentata*, *Psidium cattleyanum*, *Psychotria comorensis* et *Weinmannia comorensis*.
- le second groupe représente les espèces propres aux groupements, c'est-à-dire rencontrées dans un groupement et nulle part ailleurs. Ces espèces propres ou différentielles sont généralement peu fréquentes ou rares ; elles révèlent ainsi par leur présence une spécificité écologique de son unité et donc du biotope. Il s'agit, pour le groupe des champs par exemple, de *Artocarpus communis*, *Citrus sinensis*, *Cycas thouarsii*, *Leucaena leucocephala* et *Vitex doniana*.

La valeur indicatrice d'une espèce associe sa fidélité et sa spécificité qui représente son abondance au sein d'un groupe.

Dans le groupe G2A (forêt humide) les valeurs indicatrices sont globalement faibles. Les valeurs plus élevées sont

Tableau 2 – Indice de similarité des unités de végétation.

	Champs	G2A	G2B	G2C
Champs	1	0,36	0,45	0,3
G2A	0,36	1	0,49	0,5
G2B	0,45	0,49	1	0,34
G2C	0,3	0,5	0,34	1

attribuées à *Tambourissa comorensis* (4,7%) *Weinmannia comorensis* (3,7%) et *Ocotea comoriensis* (3,2%).

Dans l'unité G2B, correspondant à la forêt de basses altitudes, les espèces suivantes: *Nuxia pseudodontata* (7,2%) *Ocotea comoriensis* (4,37%) *Weinmannia comorensis* (4,15%) ont les valeurs indicatrices les plus élevées.

C'est dans le groupe G2C (forêt de hautes altitudes sur les coulées) que les valeurs indicatrices sont plus significatives. Elles correspondent à des espèces telles que *Apodytes dimidiata* (16,6%), *Philippia comoriensis* (15,5%), *Ocotea comoriensis* (13,99%), *Nuxia pseudodontata* (12,06%) et *Rapanea comorensis* (8,04%).

Dans les groupements de champs les valeurs indicatrices les plus élevées appartiennent à *Eugenia aromatica* (6,81%), *Mangifera indica* (4,77%), *Vitex doniana* (2,72%), *Artocarpus heterophyllus* (2,72%), *Cocos nucifera* (2,72%) et *Buddleja indica* (2,72%).

Similarité des groupes – Nous avons utilisé l'indice de similarité de Jacquard pour évaluer les ressemblances floristiques entre les unités de végétation ainsi définies (tableau 2).

Globalement la composition floristique diffère lorsqu'on va d'une unité à une autre, les indices de similarité atteignant rarement 0,5.

On note cependant une légère ressemblance (50%) au sein des groupements de la forêt, notamment (G2A-G2C), et (G2A-G2B).

Régularité et niveau d'organisation – Pour mieux comprendre l'organisation et le fonctionnement des ses unités nous avons utilisées l'indice d'équitabilité de Pielou (R).

La figure 3 montre que nous avons un peuplement très bien organisé dans les champs (R = 91%) et globalement bien organisé dans les forêts (R > 70%). Cependant on assiste à une faible diminution de l'indice de Pielou dans la



Figure 3 – Indices de régularité de Pielou (R) des unités de végétation.

forêt de basses altitudes (G2B) et dans la forêt de haute altitude sur les coulées de lave (G2C).

Paramètres structuraux quantitatifs de la végétation –

Nous avons utilisé les paramètres structuraux quantitatifs de la végétation tels que la densité (nombre d'individus/ha), la surface terrières (m²/ha), la hauteur maximale des arbres et le potentiel de régénération évalué en nombre de jeunes plants/ha, pour caractériser les unités de végétation (tableau 3).

La densité est plus élevée dans la forêt que dans les champs. Elle est aussi variable à l'intérieur de la forêt. La forte densité est notée dans la forêt des hautes altitudes sur les coulées de laves (G2C) et dans la forêt de basses altitudes (G2B).

La surface terrière qui exprime la surface d'engrègement des individus au niveau du sol est par contre plus élevée dans les champs que dans la forêt. Au niveau de la forêt elle est plus élevée dans la forêt humide (G2A) et moins élevée dans le groupe G2C.

La richesse spécifique moyenne qui témoigne de la diversité floristique est plus faible dans le groupe G2C (8,7 espèces). Elle est plus élevée dans la forêt humide (11,3 espèces) et dans la forêt de basse altitude (11,2 espèces par relevé).

Les grands arbres sont rencontrés également dans la forêt humide (28 m) et dans la forêt de basse altitude (35,5 m).

Au niveau des 78 placeaux d'inventaires 3842 plantules ont été recensés, soit en moyenne deux plantules sous chaque arbre et/ou arbuste adulte. Ces plantules sont inégalement réparties entre les groupements végétaux. C'est au niveau du groupement des champs que l'on rencontre le plus de jeunes plants (46,9%).

La faible capacité de régénération est observée dans la forêt humide (13,7%) et dans la forêt de hautes altitudes sur les coulées de lave basaltiques (15,2%).

Structure par classe de circonférence – La répartition des individus selon la grosseur diffère dans les champs, les forêts de hautes altitudes ou de basses altitudes (fig .4).

Tableau 3 – Paramètres structuraux des unités de végétation issus de l'AFC.

	Champs	G2A	G2B	G2C
Densité (ind/ha)	912	2000	2500	2942,8
Surface terrière (m²/ha)	367,4	174,5	97,5	55,7
Richesse spécifique moyenne	10	11,3	11,2	8,7
Hauteur maximale	20	28	35,5	12,7
Potentiel de régénération (%)	46,9	13,7	24,2	15,2

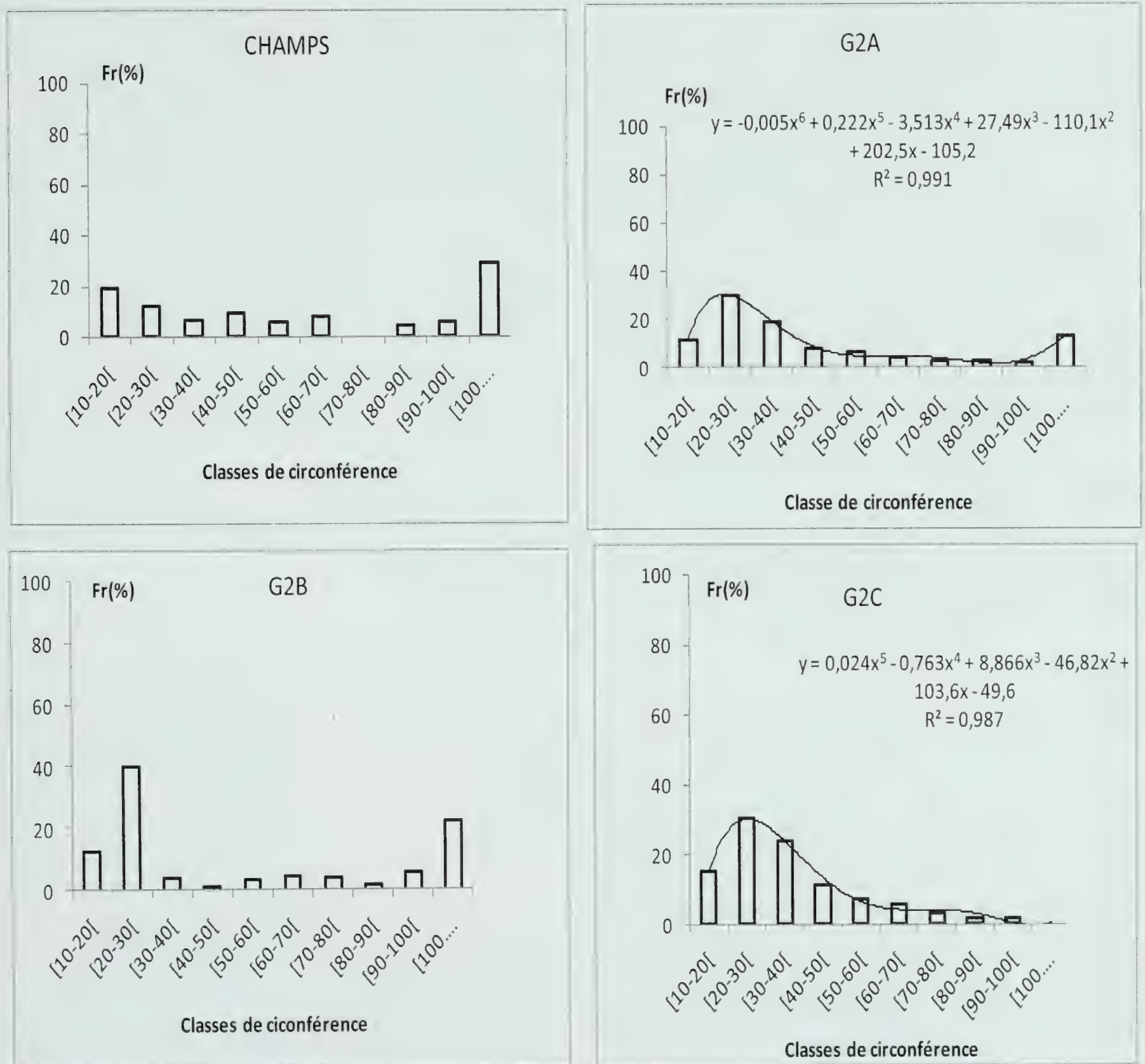


Figure 4 – Répartition des individus par classes de grosseurs dans les 4 unités de végétation.

Au niveau des champs ce sont les classes extrêmes qui sont les mieux représentées, notamment la dernière classe (28,7%) correspondant aux arbres dont la circonférence est supérieure à 1 m. Les jeunes individus regroupent 19,17% de l'effectif total du peuplement. Les classes intermédiaires sont faiblement représentées.

Le peuplement de la forêt humide (G2A) est constitué en majorité (61,8%) par des arbres dont la circonférence est comprise entre 10 et 40 cm. Les gros arbres sont faiblement représentés (9%). Nous sommes en présence d'un peuplement relativement jeune et qui régénère bien.

La courbe de distribution des arbres dans la forêt de basses altitudes (G2B) présente deux pics. Le premier pic (20–30 cm) renferme 34,7% des arbres et le second (70–80 cm) un

peu plus faible contient 16,3% des individus. Les gros individus représentent 11,7% de l'effectif total.

Au niveau de la forêt de hautes altitudes sur les coulées de laves basaltiques (G2C) les individus sont concentrés dans les cinq premières classes qui totalisent 71,5% de l'effectif total des arbres. Ce sont les individus dont les circonférences se situent entre 20 et 40 cm qui sont les plus représentés (57,2%).

DISCUSSION

Analyse globale

L'analyse globale a permis séparer nettement les champs et la forêt naturelle du Karthala.

Les champs et zones de plantation d'arbres correspondant au groupe G1 se trouvent dans les faibles reliefs et les basses altitudes ne dépassant pas 700 m. Ils sont peuplés généralement par des espèces utilisées dans l'alimentation humaine (*Cocos nucifera*, *Artocarpus heterophyllus*, *Mangifera indica*). On y trouve aussi *Eugenia aromatica* (giroflie), une espèce médicinale et aromatique exploitée comme culture de rente et *Buddleja indica*, refuge de nombreux oiseaux de basses altitudes telle que le moucheron de Madagascar *Terpsiphone mutata* (Louette et al. 2008).

La forêt dense du Karthala débute aux environs de 800 m d'altitude, elle est hétérogène et est peuplée généralement par une multitude d'espèces endémiques et autochtones dont les plus connues et les plus représentatives sont *Weinmannia comorensis*, *Ophiocolea comorensis*, *Tambourissa comorensis*, *Rapanea comorensis*.

Le sous-bois, très riche et très diversifié, est peuplé par plusieurs orchidées, pour la plupart endémiques (*Jumellea gladiator*, *Angraecum florulentum*). On retrouve aussi toute une kyrielle d'épiphytes et de fougères. (Labat et al. 1999)

Il existe également des fougères arborescentes du genre (*Cyathea*) et plusieurs lianes comme *Clematis comoresensis* et *Dioscorea comorensis*.

Analyse partielle

A l'intérieur de la forêt, la subdivision permet d'identifier trois groupements. Le taux d'information fourni par les axes factoriels plus élevés que dans l'analyse globale indique que l'on se rapproche de la réalité. Cependant, les valeurs très faibles des espèces indicatrices pour chaque groupement indiquent qu'il existe encore des difficultés pour séparer nettement les groupes. Une intégration des autres composantes de la flore permettrait d'améliorer cette analyse et de délimiter définitivement les types de végétation. Dans les forêts des basses altitudes (G2B) une espèce envahissante (*Psidium cattleianum*, Indval = 22%) domine l'essentiel du paysage entre 800 et 1000 m d'altitude. Cette espèce forme une bande bien délimitée qui parcourt la forêt d'Est en Ouest pratiquement à égale altitude. Derrière cette espèce envahissante les valeurs indicatrices les plus élevées correspondent à *Nuxia pseudodentata* (7,3%) et *Ocotea comoriensis* (4,4%).

Au dessus de la forêt de basse altitude on retrouve la forêt humide ombrophile et sempervirente (G2A) qui débute aux environs de 1100 m d'altitude, *Psidium cattleianum* y diminue sa vigueur et les espèces endémiques et autochtones deviennent de plus en plus importantes. C'est le cas de *Tambourissa comorensis* (Indval = 4,7%) et *Weinmannia comorensis* (Indval = 3,7%). Le sous-bois est peuplé par des espèces rares toutes aussi endémiques telles que *Ravenea hildebrandtii* et *Begonia comorensis*. On y rencontre plusieurs fougères arborescentes du genre *Cyathea*, une multitude de lianes, d'orchidées et d'épiphytes (fougère et autres). On appellera ce groupe, la forêt humide à *Tambourissa comorensis* et *Weinmannia comorensis*. Ce groupement, situé entre 1000 et 1800 m d'altitudes, constitue l'essentiel de la forêt du Karthala. Le sol y a évolué en sol noir forestier de type hydromorphe et les précipitations sont abondantes presque toute l'année. La diversité floristique de ce groupement reste

encore nécessite encore des investigations, notamment en ce qui concerne le sous-bois. (Labat et al. 1999).

En s'approchant du sommet du Karthala et de son caldeira gigantesque étendu sur 3 km environ, on retrouve un groupement de forêt inféodé à un substrat volcanique sur les coulées de laves basaltiques. Cette unité qui débute vers 1600 m et 1700 m selon les versants de la montagne, est proche de la brousse à Éricacées qui constitue la limite supérieure de la végétation du Karthala. Le substrat basaltique fait que l'eau ruisselle et devient peu disponible pour les plantes. Les espèces qui y sont inféodées développent des stratégies d'adaptation à ces conditions particulières. C'est le cas des feuilles charnues chez *Rapanea comorensis* et *Apodytes dimidiata*, des feuilles réduites chez *Philippia comoriensis*, *Senecio humblotii*, *Pouzolzia guineensis* et *Morella spathulata*. Les valeurs indicatrices des espèces sont très significatives. Les plus importantes sont attribuées à *Apodytes dimidiata* (16,6%) et *Philippia comoriensis* (15,5%). L'analyse de la stabilité des groupements ainsi définis a montré que le groupe G3, bien qu'il présente des particularités, notamment dans la morphologie des espèces qui y sont inféodées, est difficilement séparable du groupe G2.

Caractérisation du groupement

Paramètres structuraux de la végétation – En ce qui concerne l'altitude, le seuil à partir duquel la densité floristique et la surface terrière varient significativement est de 700 m, et correspond à la limite des champs et des zones de cultures. A partir de cette altitude la densité augmente alors que la surface terrière diminue.

En effet, l'action anthropique diminue l'effectif des arbres mais les préférences par rapport aux usages (notamment dans l'alimentation humaine, la pharmacopée et les rites traditionnels) favorisent la conservation de vieux et gros arbres dans ces zones, d'où les surfaces terrières élevées.

Dans la forêt, la densité est plus élevée en basse altitude et dans la forêt inféodée aux coulées de lave. Ceci est dû à l'action envahissante de *Psidium cattleianum* et *Philippia comoriensis* respectivement dans ces deux groupements. Dans ces deux unités, la surface terrière y est par contre plus faible pour deux raisons: premièrement ces deux espèces ont des faibles circonférences et deuxièmement, en basse altitude, plus accessibles par les populations, les gros arbres sont coupés pour leur bois. Ce sont ces deux raisons expliquent aussi le fait que l'on trouve plus de jeunes plants dans ces deux unités que dans la forêt humide. Ce modèle est aussi obtenu dans les forêts de la Réunion (Tassin et al. 2004) et dans les milieux montagnards des petites Antilles (Rousteau 1993). La richesse spécifique est aussi plus faible dans ces unités. Deux raisons sont avancées: la compétition inter-spécifique et les contraintes écologiques:

- en basse altitude tous les espaces libres sont presque automatiquement occupés par *Psidium cattleianum* au détriment des autres espèces.
- lorsque l'on monte en altitude les conditions écologiques deviennent drastiques et entraînent une diminution la richesse spécifique.

Similarité des unités de végétation – On peut mettre en évidence les activités de l’homme en comparant l’indice de similarité des champs par rapports aux différentes unités de la forêt. D’abord pour une simple question de distance, l’unité la plus proche floristiquement est la forêt de basse altitude (0,45). Elle est non seulement la plus proche mais aussi la plus accessible pour les populations. La similarité entre les champs et la forêt diminue ensuite suivant le gradient altitudinal; 0,36% avec la forêt humide et 0,30% avec la forêt des hautes altitudes sur les coulées de laves.

A l’intérieur de la forêt les indices de similarité sont faibles. Ils atteignent rarement 50%. Ceci indique à la fois une forte variabilité floristique et une grande diversité des habitats et des niches écologiques.

Structure par classes de grosseur – Dans les champs, on assiste à une anthropisation sélective qui s’exprime par la prédominance des deux classes extrêmes (jeunes plants et gros arbres). La rareté des individus dans les classes intermédiaires indique que les plantules arrivent rarement à maturité. Elles sont coupées ou élaguées pour leurs usages multiples. Les gros arbres sont conservés dans les champs soit par leur rôle fertilisant, leur ombrage ou comme bois sacré.

Dans la forêt de basses altitudes, la classe qui domine correspond à celle de la population de *Psidium cattleianum* (20–30 cm).

Dans la forêt de haute altitude et dans la forêt humide on est en présence d’une population équiennne, ou les jeunes individus sont les mieux représentés. On note cependant dans la forêt humide la présence de gros arbres (9%) sous les quelles poussent les Pipéracées (*Piper capense*) et les palmiers nains de sous bois (*Ravenia hildebrandtii*).

Potentiel de régénération – La régénération naturelle est plus élevée dans les champs et la forêt basse que dans la forêt humide et la forêt de hautes altitudes.

Dans les champs, il s’agit de jeunes plants qui poussent pendant les périodes de jachère qui ne durent pas plus de trois ans. Ils seront ensuite coupés lors des cultures et utilisés comme bois de chauffage ou bois de construction, d’où la faible densité des individus adultes (classes intermédiaires).

Au niveau des forêts basses, c’est l’effet *Psidium cattleianum*, qui influence la régénération globale du peuplement.

Régularité et structure floristique – L’indice de régularité R est élevé dans les champs (0,91). Il diminue de 0,2% entre les trois unités de la forêt. Ceci est dû à l’effet des espèces

envahissantes qui entraînent un déséquilibre dans la répartition et la croissance des individus au sein des espèces. Il s’agit respectivement de *Philippia comoriensis* dans l’unité G2C et de *Psidium cattleianum* dans G2B.

Relation entre endémisme et unités de végétation – Lorsque l’on considère l’endémicité des espèces dans les unités de végétation ainsi définies (fig. 5), on constate que pour l’endémicité large (à l’échelle de l’archipel), la forêt humide avec quinze espèces est la plus riche, suivie de la forêt basse (quatorze espèces). Les espèces endémiques de l’archipel sont faiblement représentées au niveau de la forêt de haute altitude (huit espèces) et dans les champs (cinq espèces).

La variation de l’endémicité stricte (espèces endémiques de la Grande Comore) indique que c’est la forêt des hautes altitudes sur les coulées de lave (G2C) qui contient le plus d’espèces (trois espèces), suivi de la forêt humide haute (deux espèces) et de la forêt basse (une espèce). On ne rencontre pas d’espèces endémiques strictes dans les champs. Le taux d’espèces endémiques strictes suivrait donc un gradient altitudinal croissant. Ceci semble montrer que l’intérieur de l’île est peuplé d’espèces “moins mobiles” alors que les côtes et les basses altitudes sont peuplées par des espèces “plus mobiles” dont les diaspores proviennent des côtes voisines.

CONCLUSION

Au terme de cette étude nous pouvons dire que la forêt du Karthala abrite une flore ligneuse très diversifiée, compte tenu de la variabilité des unités de végétation. Ces unités de végétations qui diffèrent par leur structure et leur diversité floristique sont tributaires de la présence/absence d’habitats et des actions anthropiques. Suivant le gradient altitudinal ont distingue dans les faibles reliefs et les basses altitudes les zones de cultures et de plantations d’arbres telles que *Cocos nucifera*, *Artocarpus heterophyllus*, *Mangifera indica*, *Eugenia aromatica*...). Au dessus de cette unité ont retrouve la forêt de basse altitude qui se situe en 800 m et 1000 m. Cette forêt est très marquée par les actions anthropiques et par l’envahissement des espèces exotiques telles que *Psidium cattleianum*, *Clidemia hirta* et *Trisetia virusanum*. La forêt humide des hautes altitudes qui débute au-delà de 1000 m, semble la plus diversifiée, la plus stable et la plus épargnée de la pression humaine. Elle est caractérisée par des espèces endémiques et autochtones (*Tambourissa comorensis*, *Weinmannia comorensis*, *Ravenia hildebrandtii* et *Begonia comorensis*). Au dessus de ce grand groupement, sur les coulées de lave proche du sommet du volcan, on retrouve un groupement de forêt très instable caractérisé par des espèces aux morphologies particulières en réponse à la précarité des conditions climatiques des hautes altitudes (*Rapanea comorensis*, *Apodytes dimidiata*, *Senecio humblottii*, *Pouzolzia guineensis*, *Morella spathulata*, *Apodytes dimidiata*). Une lande monospécifique à *Philippia comoriensis* constitue la limite supérieure de cette végétation. Dans l’ensemble, la diversité floristique est plus élevée dans la forêt humide, mais la forêt des hautes altitudes sur les coulées de lave basaltique est la plus riche en espèces endémiques du Karthala et donc de l’île. Enfin, la méthode Indval utilisée ici a permis de définir les espèces indicatrices pour chaque

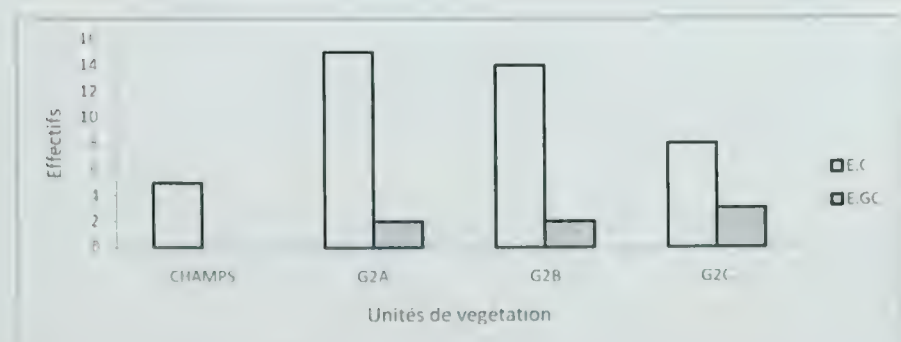


Figure 5 – Taux d’endémisme dans les unités de végétation (E.C. espèces endémiques des Comores, E.GC espèces endémiques de la Grande Comore).

unité. Ces espèces serviront dans le suivi de la dynamique spatiotemporelle de la forêt.

Pour conclure, ces résultats permettront de faciliter les plans d'échantillonnages pour les futures études sur la végétation.

MATERIEL SUPPLEMENTAIRE

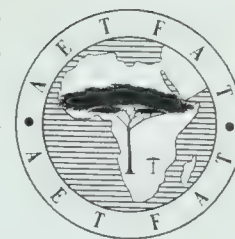
Le matériel supplémentaire est disponible au format Excel sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> > SBB50 > dossier 579) et comprend: (1) matrice de présence/absence des espèces au niveau des sites; (2) position géographique des sites et quelques paramètres de caractérisation.

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Manuscript received 30 Oct. 2010; accepted in revised version 17 Feb. 2012.

Communicating Editor: Elmar Robbrecht.



Biodiversité et valeur pastorale des herbacées de la Réserve de Fina (Mali)

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Biodiversity and pastoral value of herbaceous species of the Fina Reserve (Mali)

Background and aims – Agricultural activities and livestock pasture constitute the main human pressures on the Fina reserve in Mali. Their impacts are amplified by the bushfires and climate variations. Their impacts are amplified by bushfires and climate variability. These modifications seem to be generalized and even concern protected areas. In this context, the objective of the study was to analyze the influence of human activities on herbaceous flora diversity variation in Fina reserve.

Methods – The three classic zones of this reserve (transition, buffer zone and central area) were studied. Transition and buffer zones are disturbed environment. The central area where human activities are prohibited was used as reference for comparison. Homogenous vegetation units with similar ecological condition were identified in these three zones. On every unit, quadrats of 25 × 25 m were delimited in which four samples of 1 m² randomly distributed were carried out following the topography position.

Key results – Records include 141 herbaceous species included into 87 genera and 31 families. Poaceae family is the most represented with 25 species distributed in 18 genera. Floristic diversity is influenced by topography. The transition area is the richest, followed by the central zone and lastly by the buffer zone. The transition zone species richness is due to the abundance of adventitious plants. Perennial Poaceae regress in the Fina reserve. The herbaceous flora list of Fina reserve was established with identification of pasture species indicating disturbance. This flora list may be used as reference for vegetation dynamics studies in the Fina reserve.

Key words – Herbaceous vegetation, biodiversity, topography, Fina Reserve, Mali.

Contexte et buts – Les activités agricoles et la pâture du bétail constituent les principales pressions anthropiques sur la diversité végétale de la réserve de Fina au Mali. Leurs impacts sont amplifiés par les feux de brousse et les variations climatiques. Ces modifications ont tendance à se généraliser et même la zone centrale intégralement protégée n'est plus épargnée. L'objectif de l'étude est d'analyser l'influence des activités anthropiques sur la variation de la diversité floristique des herbacées dans la réserve de Fina.

Méthode – L'étude a porté sur les trois zones classiques d'une réserve de biosphère: transition, tampon et centrale. Les zones de transition et de tampon sont des milieux perturbés. L'aire centrale soustraite aux activités anthropiques a servi de référence pour faire une analyse comparée entre les zones. Des unités homogènes aux conditions écologiques comparables ont été identifiées dans les trois zones. Sur chaque unité, en fonction de la topographie, des placettes de 25 × 25 m ont été délimitées dans lesquelles quatre relevés de 1 m² reparties aléatoirement ont été réalisés.

Résultats-clés – Au total, 31 familles, 87 genres et 141 espèces herbacées ont été recensés. La famille

des Poaceae est la plus représentée avec 25 espèces et 18 genres. La diversité floristique est liée à la topographie des milieux. La zone de transition est la plus riche, suivie par des zones centrale et de tampon. La richesse floristique de la transition s'explique par l'abondance des adventices. Il ressort aussi que les Poaceae pérennes régressent dans la réserve de Fina. La liste floristique des herbacées a été dressée avec l'identification des espèces fourragères indicatrices de perturbation. Elle servira de base aux recherches sur la dynamique de la végétation herbacée dans la réserve.

INTRODUCTION

Le processus de dégradation qui a sensiblement entamé le couvert végétal de la réserve de Fina au Mali est la résultante de deux facteurs: les variations climatiques et les activités humaines. Les premiers sont considérés comme inéluctables à l'échelle du siècle (Fabien et al. 2006) et leurs effets actuels sur la disparition d'espèces sont généralement limités (Darkoh 2003, Wezel 2004). L'impact des activités humaines est susceptible d'être à l'origine de modifications dans l'évolution de la succession végétale et d'une dégradation du milieu (Dembélé 1996) qui peut être irréversible (Khresat et al. 1998, Darkoh 2003, Dia et al. 2008).

Jadis sous-peuplée et peu exploitée, la région du Baoulé est confrontée ces dernières décennies à une colonisation agricole par des Bambaras cultivateurs et des Peulhs éleveurs (Diallo 2004, UICN/BRAO 2008). Il en résulte une double pression pastorale et agricole caractérisée par un afflux important de troupeaux transhumants, un taux élevé de mise à culture des terres et un raccourcissement considérable de la durée des jachères (Dembélé et al. 2003). Parallèlement, les prélèvements de bois et de phytomasse sur les pâturages se sont accrus. Les feux de brousse deviennent de plus en plus fréquents et leur usage incontrôlé menace la persistance des

espèces pérennes dont ils sont censés stimuler la repousse en saison sèche. L'exacerbation de la pression foncière dans la zone de transition a eu comme conséquence une perturbation de l'équilibre des formations naturelles (Floret et al. 1994, Sanogo et al. 1995) et une perte de diversité.

Dans ce contexte, le déficit actuel pour les gestionnaires de la réserve est de pouvoir assurer non seulement un équilibre rationnel entre activités anthropiques (agricoles et pastorales) et conservation de la biodiversité, mais aussi de maintenir l'intégrité de la zone centrale de la réserve. L'action anthropique et l'impact du pâturage, en particulier, sur la biodiversité végétale fait l'objet de controverses (Daget & Poissonnet 1997, Hiernaux 1998, Achard et al. 2001, Botoni et al. 2006). Elle est tantôt considérée comme un facteur favorable à l'augmentation de la biodiversité, tantôt comme un facteur d'homogénéisation de la flore et des paysages (Botoni et al. 2006).

Cette étude visait à mesurer la variation de la diversité floristique des herbacées sous l'influence des gradients anthropique et topographique (toposéquence) de la réserve. Il s'agissait de tester trois hypothèses:

- (1) Les gradients anthropique et topographique ont une influence sur la stabilité et sur la distribution spatiale des

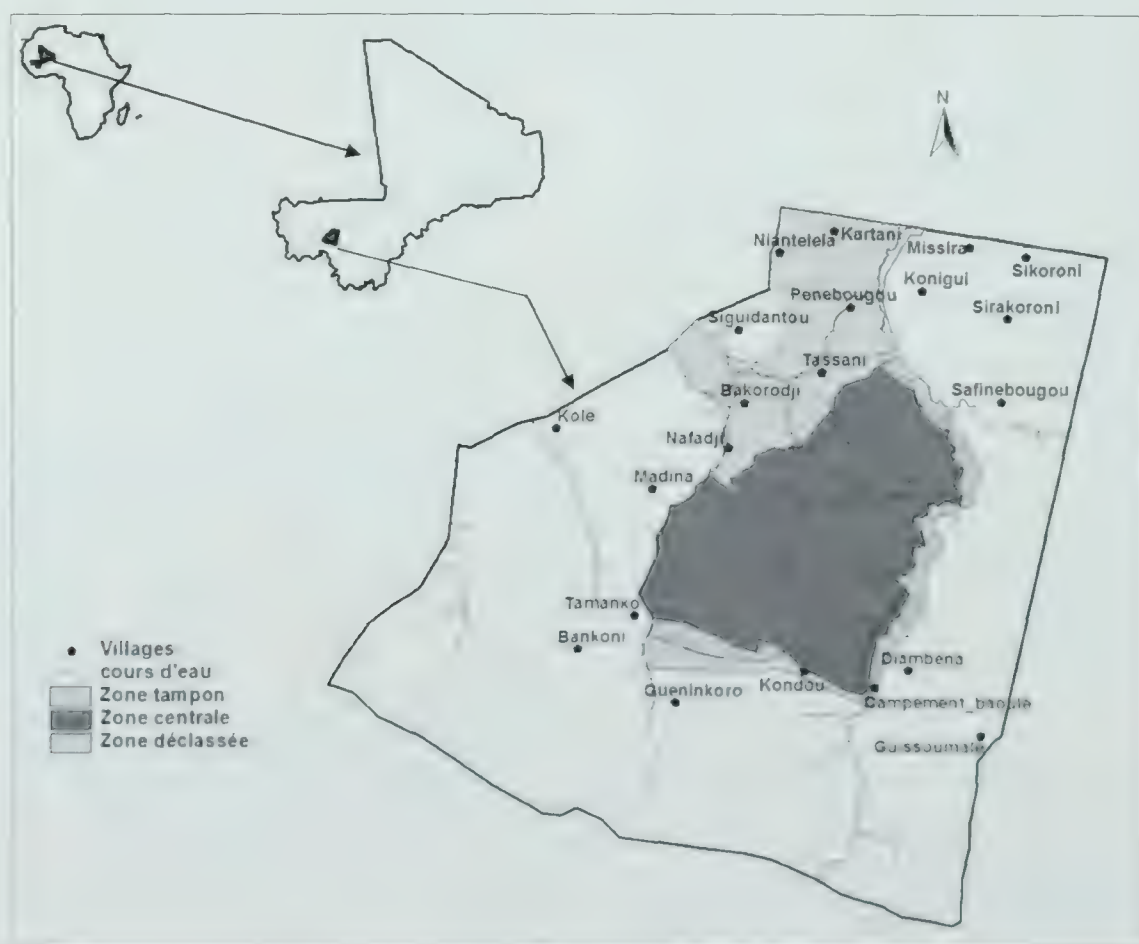


Figure 1 – Localisation de la réserve de Fina.

espèces herbacées et de leur diversité dans la réserve de Fina;

(2) La richesse spécifique en espèces pérennes diminue et a contrario la richesse en espèces annuelles croît lorsque les perturbations liées aux activités anthropiques s'accroissent.

(3) La valeur pastorale diminue avec l'augmentation de la pression anthropique surtout pastorale.

Pour ce faire, des unités de végétation topographiquement similaires ont été comparées en fonction du gradient décroissant d'influence anthropique dans la réserve: zone de transition, zone tampon et zone centrale intégralement protégée.

MATÉRIEL ET MÉTHODES

Milieu d'étude

L'étude a été conduite dans la réserve de Fina, une des trois réserves adjacentes de la réserve de biosphère de la boucle du Baoulé. Celle-ci est située à 70 km au Nord-Ouest de Bamako (fig.1), entre 13°10' et 13°40' de latitude Nord et 9°30' et 9°50' de longitude Ouest. Elle couvre une superficie d'environ 668 405 ha de zone protégée, 28 000 ha de zone de tampon et 860 000 hectares de zone de transition. En 1993, l'aire centrale de la réserve de Fina a fait l'objet d'un déclassement et sa superficie est passée de 136 000 ha à 108 668 ha. Malgré ce déclassement, cette zone continue de subir des pressions foncière et animale très fortes.

La pluviométrie dans le Fina est monomodale avec des pluies entre les mois d'avril et octobre et une moyenne annuelle de 1 100 mm au Sud et de 900 mm au Nord avec des variations annuelles à la baisse (Bosma et al. 1996) entre 400 et 1 200 mm (Nasi 1994). La température moyenne annuelle est comprise entre 26°C et 31°C avec une amplitude thermique diurne de 5° à 10°.

La réserve de Fina repose sur un plateau gréseux, caractérisé par des sols peu profonds, rocheux ou latéritiques. Au pied du plateau on trouve parfois des glacis. Les niveaux intermédiaires et bas sont difficiles à distinguer et présentent la forme de petits plateaux et de *bowés*. Entre les plateaux existent à certains endroits des vallées à hydromorphie temporaire. Au pied du plateau, on trouve des plaines assez étendues de sols ferrugineux tropicaux de texture sableuse ou argilo sableuse de couleur jaune et ocre avec des cuirasses latéritiques dans la direction de l'affluent Baoulé. Tout le long de l'affluent, on retrouve presque toujours une haute terrasse de 5 m à 8 m élevée au-dessus de son lit d'une largeur de 100 à 2000 m.

Le Nord de la Réserve est constitué par la savane soudanienne septentrionale dominée par les Combrétacées et où le tapis herbacé est caractérisé par l'absence ou la rareté des graminées pérennes. Au sud se trouve la savane soudanienne méridionale à *Isberlinia doka* (Heringa et al. 1988). Le long des cours d'eau on retrouve des galeries forestières.

Méthodologie

Quatre faciès ou unités de végétation (plateau, glacis, plaine et vallée), ont été définies et identifiées sur le terrain dans

chacune des trois zones de la réserve qui sont soumises à des régimes de protection différents: la zone centrale intégralement protégée, la zone de tampon à usage contrôlé (accès permis pour mener des activités compatibles avec des pratiques écologiquement viables), la zone de transition à usage multiple et non contrôlé (libre d'accès et toutes les activités socioéconomiques y sont permises). Les zones de tampon et de transition sont considérées comme des zones anthropisées ou perturbées et la zone de référence comme un milieu naturel non perturbé.

Sur chacune des unités homogènes repérées, des placettes de 25 × 25 m soit 625 m² ont été délimitées. La strate herbacée a été inventoriée au moyen de 5 sous-placettes de 1 m² placées aléatoirement au sein de chaque placette. L'agencement des relevés était de 5 sous-placettes × 12 placettes × 4 unités de végétation × 3 zones.

Les relevés de végétation ont été réalisés en fin d'hivernage (Septembre à Octobre 2008) correspondant à la période de pic de végétation. Les relevés sont réalisés selon les principes de la méthode sigmatiste fondée sur l'homogénéité stationnelle et l'utilisation du caractère présence/absence des espèces. A chaque espèce rencontrée, est affecté un coefficient d'abondance-dominance selon l'échelle de Braun-Blanquet (Kent & Cocker 1992).

Les indications relatives aux stations ont été également notées, en particulier la situation topographique, le type de sol, la pression de pâturage et l'action anthropozoogène.

Le spectre biologique qui indique le taux de chacun des types biologiques définis par Raunkiaer (1934) dans la flore stationnelle a été utilisé pour l'analyse de la structure verticale de la flore. Le spectre biologique, exprimé en pourcentage de chaque type biologique, caractérise la formation végétale, son origine, ses perturbations.

Calculs et analyses statistiques

Les données d'inventaire ont été traitées avec les programmes Excel pour le tableau dynamique croisé relevés/espèces et la similarité des unités topographiques des trois zones, Statistica pour la vérification de la normalité de la distribution des relevés et l'analyse de la variance.

Pour chaque zone et chaque unité végétale, la fréquence relative (FR_i) et la contribution spécifique (CS_i) des espèces au sein des relevés ont été calculées au moyen de la formule suivante:

FR_i (%) = Nombre de placettes où l'espèce i est présente sur le nombre de placettes relevées × 100

$$CS_i (\%) = \frac{FR_i}{\sum FR_i} \times 100$$

La diversité floristique de chaque unité végétale dans chaque zone a été appréciée à l'aide des indices de diversité (H') de Shannon-Weaver et de l'indice de régularité R de Pielou (1966)

$$H' = \sum_{i=1}^S p_i \log_2 p_i$$

$$R = \frac{H'}{H'_{\max}} = \frac{H'}{\log_2 S}$$

Où p_i représente l'abondance relative de l'espèce i et se calcule ainsi:

$$p_i = n_i/N$$

Où n_i = nombre d'individus de l'espèce i dans l'échantillon et N = nombre total d'individus de toutes les espèces dans l'échantillon. S est le nombre total d'espèces.

L'indice H' varie en fonction du nombre d'espèces et des effectifs de chacune des espèces.

L'indice R varie entre 0 et 1. Il tend vers 1 lorsque chacune des espèces est représentée par le même nombre d'individus et vers 0 lorsque la majorité des effectifs correspond à une seule espèce (Ramade 1987).

Le coefficient de similarité de Sorensen (C_s) a également été utilisé pour comparer la composition des unités de végétation entre les différentes zones de la réserve:

$$C_s = \frac{2a}{(2a + b + c)}$$

a = les espèces communes aux deux unités

b = richesse propre à la première unité

c = richesse propre à la seconde unité

Lorsque le coefficient calculé est supérieur à 50%, on en déduit une similarité entre les unités comparées. La similarité augmente avec la valeur de ces indices. La classification hiérarchique ascendante utilisant la méthode de Ward (1963) a permis de faire la typologie des unités de toposéquence dans les trois zones.

La vérification de la stabilité de la flore (impact du pâturage) dans les trois zones est faite à partir de la courbe "J" de Raunkiaer et de Kenoyer. Cette courbe, est un bon indicateur de la stabilité de la flore d'une zone selon Sampson (1952) et Sawadogo (2004). La connaissance du nombre d'espèces et de leurs fréquences permet d'établir cette courbe qui distingue les espèces en cinq classes de fréquence qui sont: A = 0–20%, B = 21–40%, C = 41–60%, D = 61–80%, E = 81–100%. Le groupement est dit:

- stable si $A > B > C \geq$ ou $\leq D < E$, traduisant une courbe monomodale;

- perturbé si cet ordre n'est pas respecté, la courbe est bimodale ou plurimodale.

Enfin, la valeur pastorale (VP) de chaque unité végétale dans chaque zone a été calculée en additionnant le produit des contributions spécifiques des diverses espèces au couvert végétal avec un indice de qualité (I_s) variant entre 0 (mauvais) et 5 (excellent) attribué à chaque plante (Liste floristique en annexe) en fonction de son caractère pérenne, de sa palatabilité et de sa productivité (valeur alimentaire). Karembé (2001) a utilisé la même méthode pour déterminer l'indice de qualité dans la même zone d'étude et qui prend en compte ces trois qualités recherchées.

$$VP = \frac{1}{5} \times \sum (Csi \times I_s)$$

RÉSULTATS

Diversité floristique globale

Les investigations floristiques dans la réserve de Fina ont permis de relever 141 espèces (appendice électronique 1) appartenant à 31 familles et 87 genres. Les sept familles les plus représentées comptent 65% des espèces recensées: les Poaceae avec 39 espèces (28%), les Fabaceae avec seize espèces (11%), les Asteraceae et les Convolvulaceae avec neuf espèces chacune (6%), les Rubiaceae avec sept espèces (5%), les Acanthaceae et les Amaranthaceae comptent chacune six espèces soit 4%. Les 22 autres familles regroupent 49 espèces soit 35%. Les dicotylédones y comptent 95 espèces soit 67%, les Monocotylédones regroupent 46 espèces soit 33%.

Diversité taxonomique par zone

La zone de transition se classe première du point de vue richesse en espèces, genres et familles avec 75 espèces (31%), 59 genres (31%), 24 familles (28%), suivent ensuite la zone de référence avec 72 espèces (25%), 47 genres (25%), 22 familles (26%) et la zone tampon avec 57 espèces (23%), 44 genres (23%) et 22 familles (26%). En termes de diversité spécifique c'est la zone de référence qui est la plus riche avec 29 espèces, suivi de la zone de transition avec 24 espèces et la zone tampon avec dix espèces.

Seize espèces sont communes aux trois zones et représentent près de 9% du total dont les plus abondantes sont *Andropogon pseudapricus*, *Pennisetum pedicellatum*, *Monechma ciliatum*, *Spermacoece stachydea*, *Andropogon gayanus*.

Du point de vue du nombre d'espèces par famille dans les zones, c'est celle des Poaceae qui est la plus importante avec une moyenne de plus de dix espèces dans chacune des zones. Cet effectif est plus élevé dans la zone de transition avec 22 espèces et seize genres, et diminue progressivement en évoluant vers les deux autres zones: tampon avec 21 espèces et quatorze genres, référence avec vingt espèces et seize genres.

Spectre des types biologiques

Le spectre des types biologiques (fig. 2) indique que les thérophytes (Th) sont les plus abondants avec 111 espèces soit 73%. Les hémicryptophytes, les chaméphytes et géophytes représentent respectivement 12%, 11% et 4% des espèces.

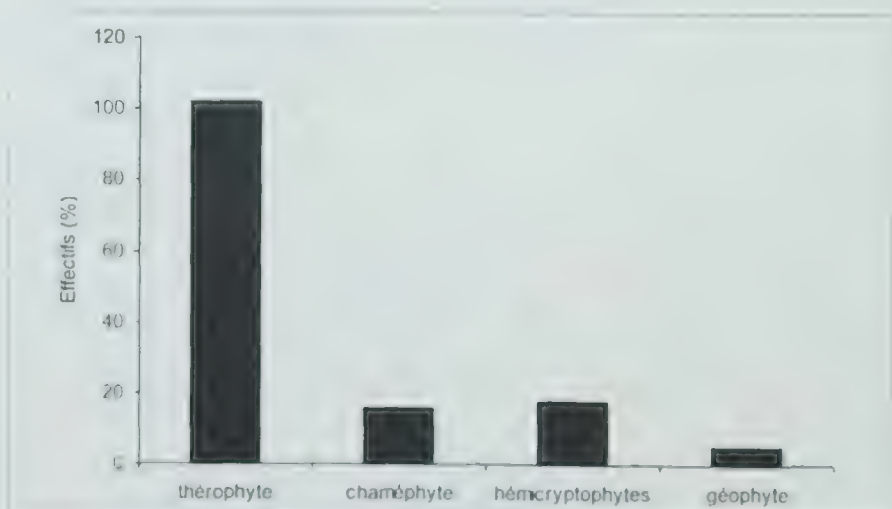


Figure 2 – Spectre des types biologiques.

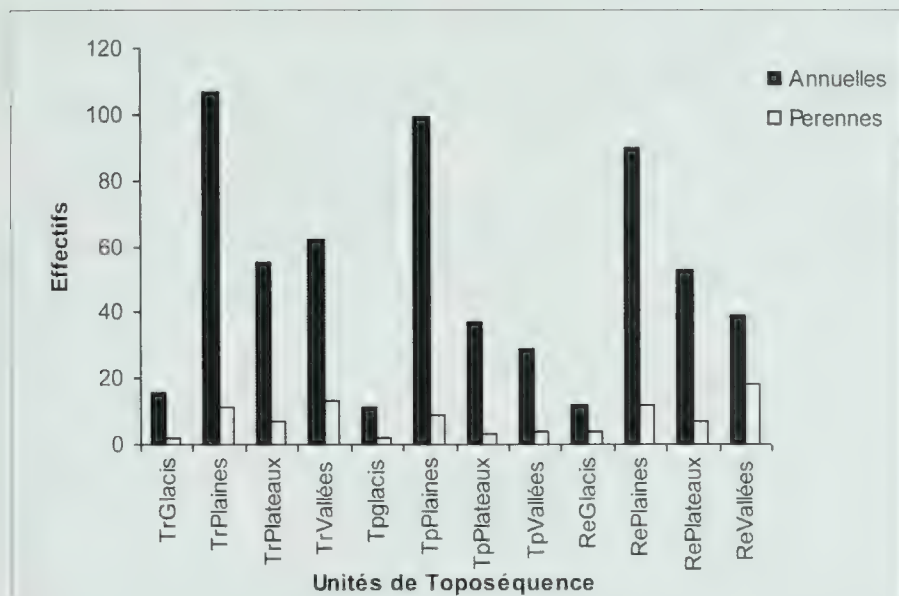


Figure 3 – Répartition par unités topographiques des annuelles et pérennes. Tr : zone de transition, Tp : zone tampon, Re : zone de référence.

Les annuelles ou thérophytes au nombre de 111 espèces (73%) sur un total de 141 effectuent leur cycle pendant la saison des pluies et disparaissent en Septembre–Octobre, après avoir bouclé leur cycle végétatif (après la fructification). Les graines assurent la régénération des espèces, après avoir traversé la saison sèche à l'état de vie ralentie (Poilecot 1999).

Contrairement aux annuelles, les herbes pérennes selon Poilecot (1999), au nombre de trente (21%) sont adaptées pour survivre aux conditions difficiles de la saison sèche. La présence de parties végétatives résiduelles et d'un système racinaire puissant permet la repousse de ces plantes dès le retour de la saison des pluies.

La figure 3 représente la fréquence de présence des espèces annuelles et pérennes suivant la topographie et par zone. Les espèces annuelles sont plus abondantes que les espèces pérennes, et sont plus présentes dans les plaines en zone de transition, suivie des zones de tampon et de référence. Les plantes pérennes sont plus représentées dans les vallées de la zone de référence, zone où sont exclues les activités anthropiques. Il semble donc que la pression anthropique favorise plutôt la présence d'espèces annuelles, tandis que la protection (zone de référence) favoriserait la présence d'espèces pérennes. Dans les unités de plateaux et glacis, destinées généralement au pâturage dans la zone de transition, l'effectif des espèces annuelles et pérennes est faible. Ce même constat est visible dans les zones de référence et de tampon.

Analyse de variance

L'analyse de la variance a porté sur les relevés des unités topographiques de chacune des trois zones (fig. 4). La variance observée des espèces annuelles et pérennes entre les unités topographiques révèle une différence entre les unités de plaine, de glacis et de plateau en zone de référence comparée aux mêmes unités dans les zones de tampon et de transition ($p < 0,01$). Par contre les unités de vallée des trois zones sont semblables dans leur composition floristique ($p = 0,68$).

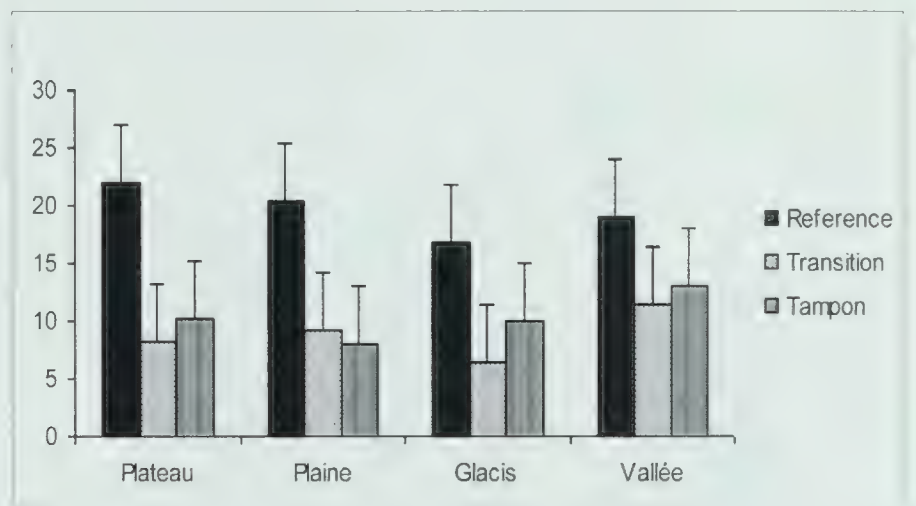


Figure 4 – Variance des espèces annuelles et pérennes observée entre les unités topographiques dans les trois zones.

Diversité spécifique, caractéristiques structurales et stabilités des formations herbacées des unités topographiques des trois zones

Diversité spécifique et caractéristiques structurales – Dans les trois zones suivant les types d'unités topographiques, on remarque une différence entre les formations végétales. La savane arborée est surtout observable dans la zone de référence. Les zones de transition et de tampon exceptées, certaines unités de vallées à galeries forestières sont surtout caractérisées par des savanes arbustives et des savanes parcs (champs et jachères).

L'appendice électronique 2 présente les espèces les plus abondantes et les grandeurs de la diversité spécifique des principales formations végétales réparties sur les différentes unités topographiques. Excepté sur les unités de plateau en zone de référence, la richesse spécifique est plus élevée sur les unités de vallées et de plaines des zones de transition et de tampon qui constituent des milieux anthropisés ($p < 0,001$). L'augmentation de la richesse spécifique moyenne dans les unités de vallées et de plaines en zone de transition montre une présence importante d'espèces herbacées inféodées aux activités anthropiques en particulier les adventices des cultures.

L'examen de la variation de la diversité par unité topographique dans chacune des zones révèle que l'indice de diversité de Shannon est plus élevé sur les unités de vallées, et de plaines des milieux de la zone de référence avec respectivement 2,51 et 2,46 bits. Par contre, sur les unités de vallées comparées aux unités de transition, cet indice est légèrement inférieur: 2,44 bits contre 2,46 bits. Les formations des unités de la zone de tampon présentent les plus faibles valeurs, certainement du fait de l'impact des activités agricoles (notamment l'activité pastorale) sur la diversité floristique.

L'indice de régularité de Piélou est dans l'ensemble des unités topographiques des trois zones supérieure ou égale à 0,85 bits excepté pour l'unité de glacis de la zone de transition, plus faible avec 0,67 bits. Cela semble indiquer une forte dominance d'une ou de deux espèces au niveau de cette unité de glacis présentant une diversité qui équivaut à 67% contre au moins 85% pour les autres unités de l'entropie maximale à l'échelle de Shannon.

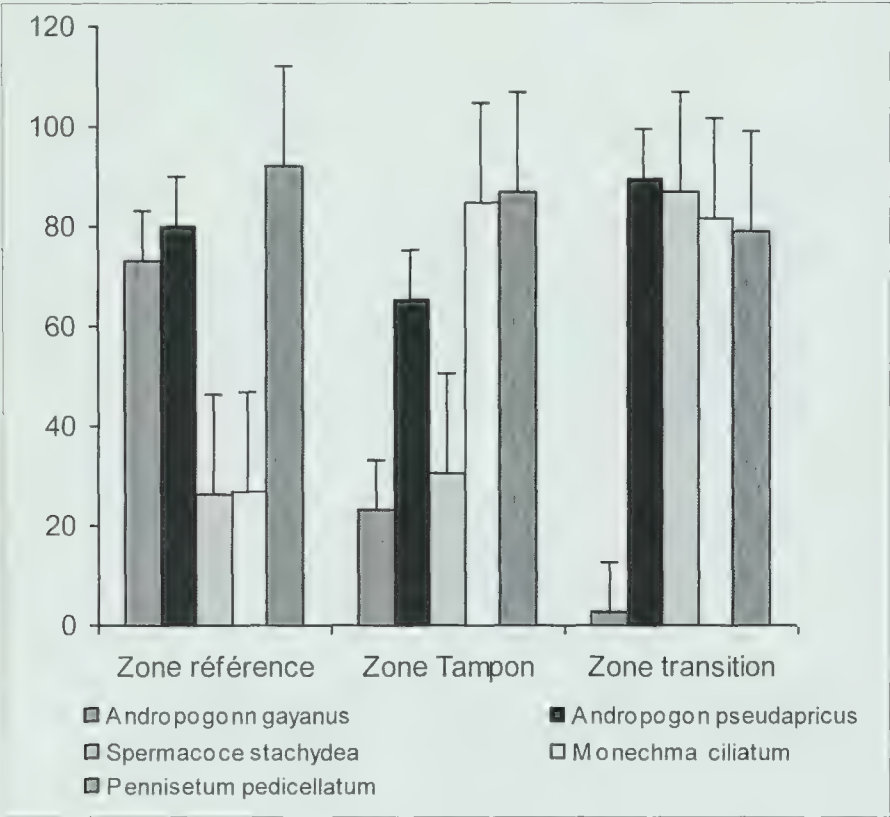


Figure 5 – Variation de la présence de 5 principales espèces herbacées dans les trois zones.

Les valeurs pastorales moyennes calculées par unité topographique à partir des indices sont variables. Sans surprise, c'est dans les unités de vallées et de plaines dans les trois zones que les valeurs pastorales sont importantes. Les valeurs pastorales comparées dans les unités de même nature des trois zones indiquent que les herbages dans la zone de référence sont les plus importants, suivis par ceux des zones de transition et de tampon. A l'échelle des zones, cette valeur pastorale est de 59,82% en zone de référence, 48,55% en zone de tampon et 49,07% en zone de transition. Les résultats obtenus montrent de façon générale que la valeur pastorale des pâturages est corrélée non seulement à l'unité de végétation (les unités de vallées, généralement humides de par leurs positions topographiques, favorisent l'augmentation de la valeur pastorale), mais également à la pression pastorale proprement dite: plus cette pression diminue, plus la valeur pastorale augmente.

Il ressort de l'observation et de l'analyse des données rapportées que le recouvrement du sol est moins important sur les unités de glacis à sols gravillonnaires et à certains endroits des unités de plateaux à sols rocaillieux et gravillonnaires aussi bien en zone de transition qu'en zones de tampon et de référence. C'est sur les unités de plaines et de vallées dans les trois zones qu'on rencontre un fort recouvrement du sol par les herbacées.

Dans toutes les zones, sur les quatre unités (plateau, plaine, glacis et vallée), se trouve un fonds commun d'espèces avec peu de graminées pérennes dont les plus remarquables sont: *Andropogon gayanus*, *Andropogon pseudapricus*, *Pennisetum pedicellatum*, *Spermacoce stachydea* et *Monechma ciliatum*.

L'analyse de la variation des fréquences de ces cinq espèces communes aux trois zones (fig. 5) révèle que de la zone de référence à la zone de transition, il est noté une nette régression de la présence d'*A. gayanus* (73,3% à 2,6%). *P. pedicellatum* a également une présence régressive de la zone

Tableau 1 – Calcul du coefficient de Sorensen entre les trois zones pour chaque type d'unité.

Tr: Transition; Tp: Tampon; R: Référence; V: Vallée; G: Glacis; PP: Plaine; LG: Plateau.

Unités	RG	RLG	RPP	RV	TpG	TpLG	TpPP	TpV
TpG	0,39							
TpLG	0,3	0,34						
TpPP	0,25	0,27	0,19					
TpV	0,37	0,33	0,35	0,35				
TrG	0,25	0,29	0,21	0,29	0,42			
TrLG	0,26	0,32	0,25	0,33	0,35	0,31		
TrPP	0,28	0,27	0,28	0,32	0,57	0,34	0,41	
TrV	0,33	0,35	0,29	0,36	0,48	0,32	0,45	0,35

de référence 92,3% à la zone de tampon 86,6% et de transition 80%. Par contre les espèces herbacées comme *A. pseudapricus*, *S. stachydea* ont une présence élevée dans la zone de transition avec respectivement 89,5%, 79% et régressent progressivement en zone de tampon et de référence. Quant à *M. ciliatum*, de 2,6% faible en zone de référence passe en zone de tampon à 84,6% et en zone de transition à 81,6%.

Stabilité de la flore – Les résultats fournis par les courbes de Raunkiaer et de Kenoyer (fig. 6) révèlent une perturbation de la flore dans l'ensemble des unités topographiques des zones de transition et de tampon (exceptée l'unité de plateau), comme en témoigne l'allure de la forme bimodale des courbes Raunkiaer et de Kenoyer relatives aux deux zones. En revanche, dans la zone de référence et sur l'ensemble des unités, la flore au regard de la forme unimodale des courbes est stable donc faiblement perturbée.

Similarité entre les unités des trois zones

Les coefficients de similarité qui comparent la présence des espèces sur les unités de végétation de même type topographique (exemple: tampon glacis, référence glacis, transition glacis) des trois zones (tableau 1) sont inférieurs à 50%. Cette dissimilitude est surtout marquée non seulement entre les unités de plaine de la zone de référence et de la zone de tampon avec comme valeur 19% mais aussi entre les unités de plaine de la zone de référence et de la zone de transition avec comme valeur 28%. Par contre à l'intérieur de chacune des zones, les quatre unités de végétation présentent entre elles une certaine similarité. Cette similarité est plus élevée entre les unités dans la zone de référence avec une valeur moyenne supérieure à 70% contre une valeur moyenne de 51% et 49% respectivement en zone de tampon et de transition. A l'échelle des zones, la dissimilarité inter zonale est plus forte entre la zone de référence et la zone de transition (fig. 7).

DISCUSSION

Les inventaires floristiques ont permis de dresser une liste de 141 espèces, 87 genres et 31 familles dans la réserve de Fina. Ce chiffre relativement appréciable montre que, malgré les perturbations constatées, la réserve demeure encore riche

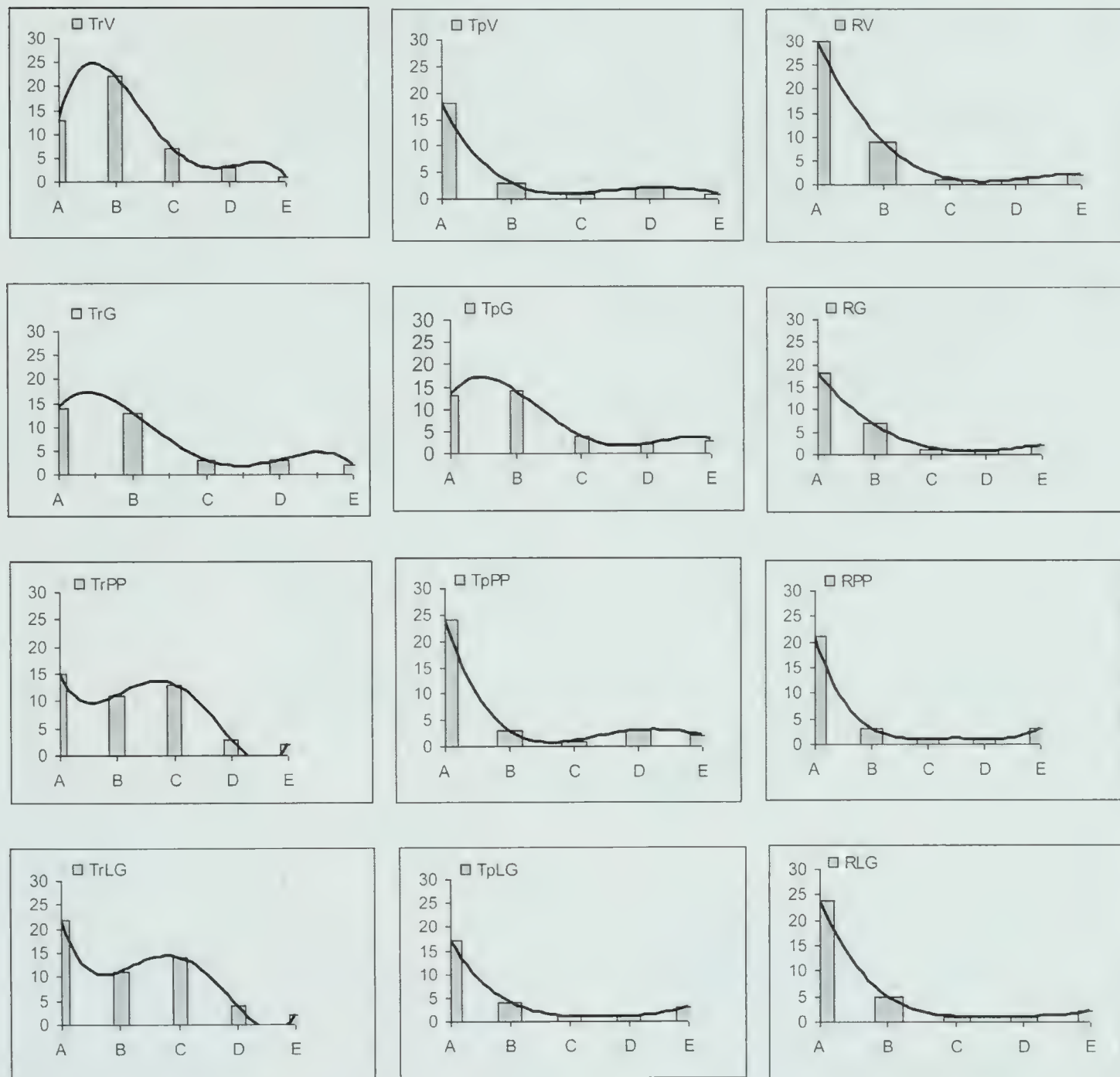


Figure 6 – Courbe de fr quence de distribution des esp ces dans les zones de transition, Tampon et de R f rence. A, B, C, D et E repr sentent les centres des classes de fr quence. Tr : Transition ; Tp : Tampon ; R : R f rence ; V : Vall e ; G : Glacis ; PP : plaine ; LG : Plateau. Les chiffres en ordonn e repr sentent le pourcentage d'esp ces pour les diff rentes classes de fr quence.

et diversifi e en esp ces herbac es. L'examen de la flore en fonction des gradients topographique et anthropique fait ressortir la richesse sp cifique plus  lev e dans la zone de transition d di e aux activit s agricoles et pastorales. Cette richesse r sulte non seulement des activit s courantes de cultures mais aussi de l'h ritage des cycles culturaux pr c dents dans les jach res et de la capacit  de nombreuses esp ces postculturaux   se maintenir sous l'effet perturbateur du p turage.

La faible richesse en esp ces de la zone de tampon comparativement aux zones de r f rence et de transition s'explique par le fait qu'elle couvre une bande qui longe les deux cours d'eau: l'affluent Baoul  et le d fluent K ni . Cette position l'expose   une forte pression de p turage. D s l'arr t des pluies, tous les transhumants qui arrivent dans la zone, campent non loin de ces cours d'eau pour l'abreuvement des animaux. Cette situation entra ne in vitablement une d gradation des sols due au pi tinement des animaux dont l'effectif pour le seul b tail transhumant est estim    300 000 t tes /an avec un taux annuel de croissance de 2% (K b  1994) soit un surplus annuel de 9 000 t tes (Diallo 2004). Cette croissance est un signe de pression de p ture,

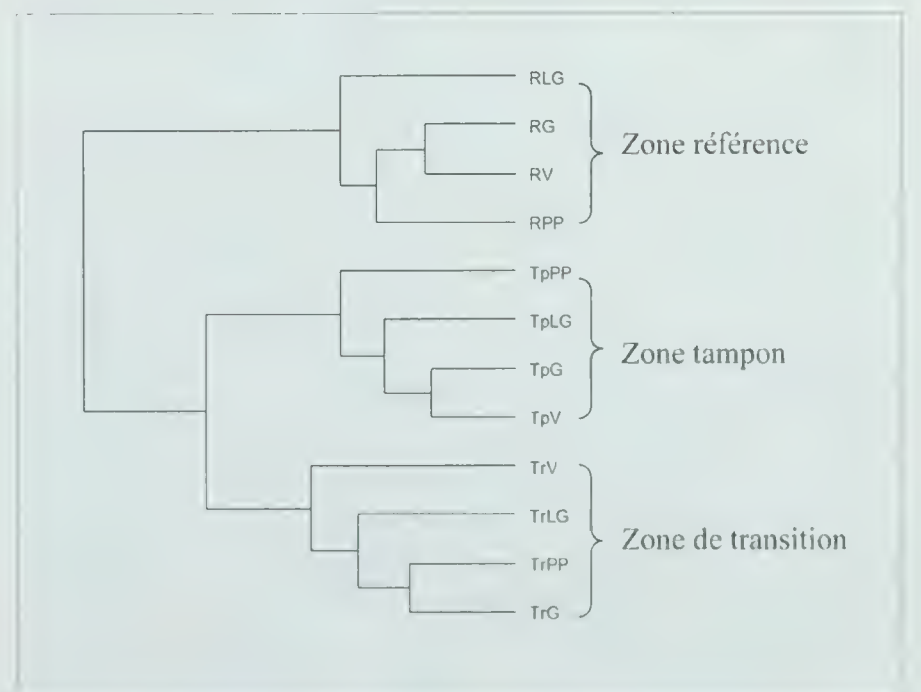


Figure 7 – Dendrogramme de Ward's method indiquant la dissimilarit  entre les unit s topographiques dans les diff rentes zones de la r serve de Fina. R : R f rence, Tp : Tampon, Tr : Transition ; LG : plateau, G : Glacis, V : Vall e, PP : Plaine.

eu égard à la baisse de la biomasse consécutive à l'extension des cultures et à l'irrégularité des pluies.

L'abondance des zones de transition (en situation de forte pression) et de tampon (en situation de pression modérée) en herbacées annuelles sur toutes les unités topographiques et particulièrement les unités de plaines est une indication de dégradation possible des parcours. Cela est cohérent avec la faible présence des espèces pérennes (trente seulement) surtout rencontrées dans la zone de référence (en situation de faible pression). Ces espèces pérennes occupent surtout les plaines et les vallées.

Le rapport entre espèces annuelles et espèces pérennes révèle un taux plus élevé dans les zones de transition et de tampon en comparaison avec la zone de référence. Plus le taux (rapport annuelles / pérennes) est élevé, plus la pression sur les ressources est forte (Jauffret 2001). Ce taux élevé est donc révélateur de perturbations liées aux activités humaines et pastorales dans les zones de transition et de tampon comme en témoigne la présence des espèces rudérales (plantes qui colonisent les sites perturbés) et ségétales (plantes qui poussent typiquement en association avec les cultures). L'importance des espèces annuelles (thérophytes) dans les trois zones, est donc un signe de déséquilibre, défavorable aux graminées vivaces, entraînant donc une dégradation des sols et de la végétation surtout pastorale. Nos résultats s'accordent avec les travaux de Botoni et al. (2006) en zone ouest du Burkina Faso et confirment les connaissances scientifiques actuelles concernant l'effet de la dégradation qui favorise les espèces annuelles (Quézel 2000, Jauffret 2001). Ceci se répercute finalement sur la valeur pastorale dont les indices issus de notre analyse sont pratiquement identiques à ceux proposés par Dembélé (1996) pour la même zone d'étude. C'est dans les zones de transition et de tampon sur les unités de glaciés et de plateaux que la valeur pastorale et la fréquence de présence des pérennes ont été faibles.

La valeur pastorale, selon Daget & Poissonnet (1971), Boudet (1978), Le Houérou (1980) est très variable, car liée à plusieurs facteurs qui sont eux-mêmes variables dans le temps et dans l'espace. Les activités agricoles, le surpâturage, les feux de brousse tardifs qui ravagent les savanes chaque année sont les causes probables de la régression des espèces pérennes au profit des espèces annuelles. En effet, selon Kagone (2000), dans les savanes soudaniennes, une pression de pâture trop forte peut expliquer l'absence ou plutôt la régression des graminées pérennes. La faible présence de ces graminées atteste de la faible capacité des pâturages à produire des repousses après le passage des feux précoces et dès l'arrivée des premières pluies. Des résultats similaires ont été évoqués par Botoni et al. (2006) dans la zone ouest du Burkina Faso. Ces auteurs ont montré que la valeur pastorale des pâturages baissait avec l'augmentation de la pression pastorale et cela à cause de la diminution de la contribution des bonnes espèces fourragères. Kiéma (2007) a indiqué que les graminées pérennes productrices sont presque totalement éliminées en zone de pression forte (zone de transition) alors qu'elles sont relativement encore bien présentes dans la zone où la pression est faible (référence).

Certaines espèces peuvent être indicatrices de changements abiotiques (état du milieu) et biotiques (niveau de per-

turbation ou de dégradation) (Arbonnier 2002). La présence exclusive de *Loudetia togoensis* sur les glaciés et les plateaux à sols gravillonnaires indique leur préférence des sols peu profonds et fréquemment soumis aux feux de brousse. *Monechma ciliatum* et *Spermacoce stachydea* sont des adventices de cultures fréquentes dans les champs et qui persistent également dans les jachères. Ces deux espèces selon Botoni et al. (2006) sont indicatrices d'épuisement des parcours. Leur fréquence augmente corrélativement avec l'intensification des activités anthropiques et diminue lorsqu'on progresse vers la zone de référence. Cette diminution de fréquence est également constatée au fur et à mesure qu'apparaissent les espèces comme *Pennisetum pedicellatum* et *Andropogon pseudapricus*. Ces deux espèces semblent indiquer non seulement la perturbation du milieu mais aussi la dégradation des sols.

A. pseudapricus tolère les perturbations et surtout les passages réguliers des feux de brousse. Par ailleurs, elle est considérée comme caractéristique du stade 'climacique' de la succession herbacée des zones régulièrement brûlées (Yossi 1996). Par contre, *P. pedicellatum* est plutôt une espèce sensible aux perturbations liées surtout aux feux et est moins abondante sur les unités où les feux ont passé. *P. pedicellatum* est d'ailleurs considérée comme indicatrice d'un retour de fertilité des sols des jachères aux yeux des paysans.

La diminution progressive d'*Andropogon gayanus* et la quasi absence de *Cymbopogon giganteus* semblent être dues à la baisse de la pluviométrie de ces dernières années et à la forte pression de fauche à laquelle elles sont sujettes en raison de leur utilisation dans la construction avant même qu'elles ne bouclent leur cycle biologique et la pression de feux et de pâture pour stimuler les souches en saison sèche pour des repousses fraîches. Des études réalisées au Mali par Cissé (1980), Penning de Vries & Djiteye (1982) et Karembé (2001) ont établi le même constat, de même que par Djiteye (1984) qui a indiqué en plus que cette régression se faisait du nord vers le sud du pays. La présence de *Cochlospermum tinctorium* sur l'ensemble des unités en zone de référence et sur les unités de plateaux en zone de tampon et de transition témoigne d'un passage régulier de feux.

La zone de référence, malgré sa protection intégrale présente certaines adventices entre autres *M. ciliatum* et *S. stachydea*, des espèces du genre *Eragrostis* qui sont indicatrices de traces d'activités humaines et notamment la présence frauduleuse du bétail, qui à travers les bouses peut y disséminer les graines des herbes broutées dans la zone de transition. Ce sont donc des signes de violations de cette zone de référence par le bétail à certains endroits, et la dissémination de ces adventices a tendance à fragiliser le maintien d'autres espèces (par exemple pérennes).

Du point de vue de la diversité structurelle, le nombre de genres communs dans les trois zones est relativement plus élevé que le nombre de genres spécifiques à chaque zone. Ceci témoigne de leur appartenance au même écosystème. Les familles les plus représentées en nombre d'espèces dans ces unités sont: les Poaceae, les Fabaceae, les Convolvulaceae et les Asteraceae. Plusieurs auteurs s'accordent sur la prédominance de ces familles dans la flore soudano-sahélienne (Berhaut 1967, Boudet et al. 1986, Heringa et al. 1988).

L'évaluation de la diversité sur la base du calcul des indices de diversité et d'équitabilité révèle que tous les indices de diversité calculés sont élevés. Les indices d'équitabilité sont compris entre 0 et 1. Il n'y a donc pas de valeurs extrêmes. Cela montre que sur le plan de la diversité, toutes les trois zones sont assez diversifiées en espèces herbacées, et ensuite que chaque zone compte un nombre appréciable d'espèces. Daget (2003) indique que quel que soit le biochore concerné la flore d'une station (richesse floristique ou diversité α) est considérée comme 'assez riche' lorsqu'elle renferme 31 à 40 espèces.

La diversité floristique est étroitement liée à la topographie des milieux et à la nature des sols. La comparaison entre les unités topographiques de chacune des zones montre une plus grande diversité sur les plaines et les vallées indiquant que de meilleures conditions y sont réunies.

Les valeurs de l'indice de diversité de Shannon, de l'indice d'équitabilité de Pielou attestent également cette richesse et sans une différence notable entre les unités. Il faut rappeler que lorsque l'indice d'équitabilité d'un écosystème ou d'une formation végétale dépasse 70% ce qui est le cas de chacune des unités des zones (référence, tampon et transition), on est en présence d'un milieu relativement stable (Barbault 1995). Ceci sous entend que la compétition est relativement faible entre les espèces en communauté dans les différentes unités. Ces observations semblent dans notre étude confirmées par les courbes de Raunkiaer et de Kenoyer.

L'analyse de la variance observée entre les unités topographiques des trois zones révèle une ressemblance entre les zones de transition et de tampon. Par contre, il existe une différence entre la zone de référence comparée aux zones de tampon et de transition. Les coefficients de Sorensen obtenus attestent cette différence entre les unités de même type des trois zones avec plus d'espèces différentes que d'espèces communes entre la zone de référence et les deux autres zones. Cela semble indiquer le caractère de faible niveau de perturbation de la zone de référence et de fort niveau de perturbation des zones de transition et de tampon.

CONCLUSION

L'étude a montré qu'outre l'impact de la topographie, le gradient anthropique a une influence sur la variation de la structure de la flore et de sa diversité.

Du point de vue richesse floristique, la zone de transition en situation de forte pression est plus riche que la zone de tampon (situation de pression moyenne) et que la zone de référence (situation de faible pression). La dégradation de la végétation dans la zone semble se manifester par une élimination ou une régression des graminées vivaces essentiellement et leur remplacement par des graminées annuelles en particulier les adventices de cultures. Les pressions (foncières et pastorales), qu'elles soient fortes ou moyennes favorisent l'augmentation des annuelles au détriment des pérennes. Par contre, elles diminuent la valeur pastorale. Ce qui confirme que les perturbations anthropiques augmentent la richesse spécifique, mais diminuent la part des plantes pé-

rennes et augmente celle des annuelles avec des conséquences néfastes sur la valeur pastorale.

Cette étude a aussi permis de mettre en évidence les espèces indicatrices de pressions anthropiques.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible au format pdf sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> > SBB50 > dossier 568) et comprend: (1) liste floristique des familles, nombre de genres et d'espèces herbacées recensées dans la réserve de Fina; (2) diversité et caractéristiques structurales des unités topographiques; (3) liste floristique détaillée des espèces herbacées recensées dans la réserve de Fina.

REMERCIEMENTS

Les auteurs remercient le Gouvernement de la République du Mali et la Coopération Technique Belgique pour les financements accordés à Mr Diallo Hady pour réaliser ses recherches doctorales. Nos remerciements s'adressent également aux corps professoraux de l'Université Libre de Bruxelles (Belgique) et de la Faculté des sciences et techniques de l'Université de Bamako (Mali) pour leur encadrement.

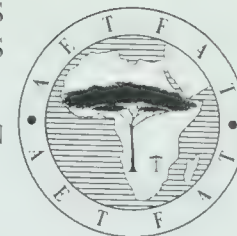
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Manuscript received 28 Oct. 2010; accepted in revised version 15 Dec. 2012.

Communicating Editor: Bonaventure Sonké.



Chromolaena odorata thickets in forest recovery in southern Cameroon

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Background and aims – Every year, large areas of tropical forests are converted to agricultural lands by the slash and burn system of cultivation. Once crops have been harvested and in order to restore soil fertility, the land is abandoned for some years, opening the way to forest recovery. The different sequences in this process depend on the duration of the fallow period. Some steps of forest recovery are dominated by dense thickets of *Chromolaena odorata*, an invasive plant species in many tropical areas. This study aims to study its role in the course of secondary succession.

Methods – The study was carried out in 144 post agricultural plots in southern Cameroon aging from six months to 35 years of age, situated along a phytogeographical gradient stretching from the coastal evergreen forest to the mixed forest in the hinterland. Floristic inventory involved recording all plant species and individuals of trees and shrubs of at least 5 cm diameter at breast height (dbh) in each plot. A multivariate analysis was performed to discriminate plant communities.

Key results – Of the 144 plots studied, thirty aged from one to five years were forming a homogeneous plant community dominated by dense thickets of *Chromolaena odorata*. These thickets are distinctive with regard to their structure, species composition and dynamics. They hamper forest recovery and it is only when stems of *Chromolaena odorata* weaken and die that succession is sped up. The former vegetation cleared before the last cropping season, the vegetation type surrounding the fallows as well as the number of farming cycles in the same plots are factors influencing secondary succession in former agricultural lands.

Key words – *Chromolaena odorata*, forest recovery, shifting cultivation, fallow, Cameroon.

INTRODUCTION

In the past decade, the annual global deforestation rate decreased from 16 million hectares in the 1990s to 13 million by 2010, South America and Africa being the two parts of the world with highest forest loss (FAO 2010). This rate despite dropping somewhat over the last two decades, still remains high. Among the many causes of deforestation in tropical countries, logging and shifting cultivation are the most important (Brown & Lugo 1990, Laurence 1999, van Gernerden 2004). These two practices are often linked in the sense that tracks opened in the forest by logging companies are afterwards used by local inhabitants to access the forest for cultivation. Shifting cultivation is a widespread practice

in tropical areas such as in Cameroon (Carrière et al. 2002, van Gernerden 2004). Among those who use a shifting cultivation system, there is often a preference for clearing secondary rather than mature forests because trees in the latter have harder wood and cutting thus requires more physical effort (Christanty 1986, Brown & Lugo 1990).

Southern Cameroon which lies within the Congo basin is covered by dense tropical rainforest. As with other tropical areas elsewhere in the world, these forests are subject to logging and pressure from cultivation. Every year during the dry season, locally referred to as ‘essep’, large areas of forest are cleared and burned. With the arrival of rains, food crops are planted and weeded. The field is abandoned after harvest and the farmer will establish another field elsewhere.

The abandonment of the cultivated land is the starting point of forest recovery, a process depending on the intensity, duration and frequency of the disturbance (Chazdon 2003). Forest recovery occurs in successional steps characterized by one or a group of species (Budowski 1965, Khan 1982, Swaine & Hall 1983, Saldarriaga et al. 1988, Finegan 1996). These steps take place gradually following an ecological continuum. There is an abundant literature on the ecological behaviour of plant species involved in forest recovery (van Steenis 1958, Budowski 1970, Vasquez-Yanes & Orozco-Segovia 1982, Swaine & Whitmore 1988, Whitmore 1989, Riera et al. 1990). However, this literature treats only dominant tree species that form pure stands in these vegetation stages (Alexandre 1978, Kahn & Namur 1978, Mosango & Lejoly 1988).

Chromolaena odorata (L.) R.M.King & H.Rob. (referred to as “*Chromolaena*” hereafter) is a gregarious herb to subshrub native from tropical America which is now invasive in most tropical areas in Africa and Asia. With shortening of the length of fallow period in the tropics, *Chromolaena* is replacing the pioneer forest species that convert herbaceous fallows into woody communities and dominates early stages of recovery after forest conversion for agriculture. The timing of its introduction in Cameroon is not well known but is supposed to have taken place either in 1937 (Muniappan et al. 2005) or in 1960 (Ngobo et al. 2004). As an invasive plant, *Chromolaena* is of major concern both to farmers and scientists. As a colonizer of disturbed areas (Epp 1987), it produces abundant wind dispersed seeds from January to March–April, just after the period during which clearing takes place. Once plant debris has been burnt, the light seeds of *Chromolaena* find suitable condition for germination, which is triggered by intense sunlight. Because of its large invasive capacity, *Chromolaena* becomes the most abundant and dominant species in the fallows. In Southern Cameroon, farmers usually shorten fallow length and prefer plots in

which *Chromolaena* is dominant, believing that it improves soil fertility since their crops do well in fields which prior to slash and burn, were dominated by this plant (Ngobo 2009). This importance of *Chromolaena* for soil fertility has been confirmed in studies by Kanmegne et al. (1999), Koutika et al. (2004), Koutika et al. (2005), and Ngobo et al. (2004), and may explain why farmers prefer to clear thickets of *Chromolaena* for farming. In some cases, *Chromolaena* is more useful as a potential fertilizer plant than some legume species such as *Calliandra calothyrsus* and *Pueraria phaseoloides* (Kanmegne et al. 1999, Koutika et al. 2005). In fallows established from fields created by clearing *Chromolaena* thickets, weed infestation is low compared to fallows emanating from natural bush (Ikuenobe & Analiefo 2003). Many studies carried out to date concern the management and biological control of *Chromolaena* (Goodall & Erasmus 1996, Zachariades et al. 2009, Delfino Abeya 2002, Muniappan et al. 2005, Koutika & Meutem-Kamga 2006, Chandrasekaran & Swamy 2010). Its role in secondary successions has not, however been sufficiently analysed. Very often the presence of this species is only mentioned as a facies of secondary succession without giving any detail on its role in forest recovery (Ngobo et al. 2004, Kassi N'Dja & Decocq 2008, Koutika & Rainey 2010). The present study aims to analyse dense thickets of *Chromolaena* in the early stages of forest recovery, with a focus on species diversity, structure and dynamics.

MATERIAL AND METHODS

Study area

This study was conducted in agricultural fields of fourteen villages of southern Cameroon, in a transect between 2°22'–2°23'N and 9°49'–11°17'E slightly north of the equator (fig. 1).

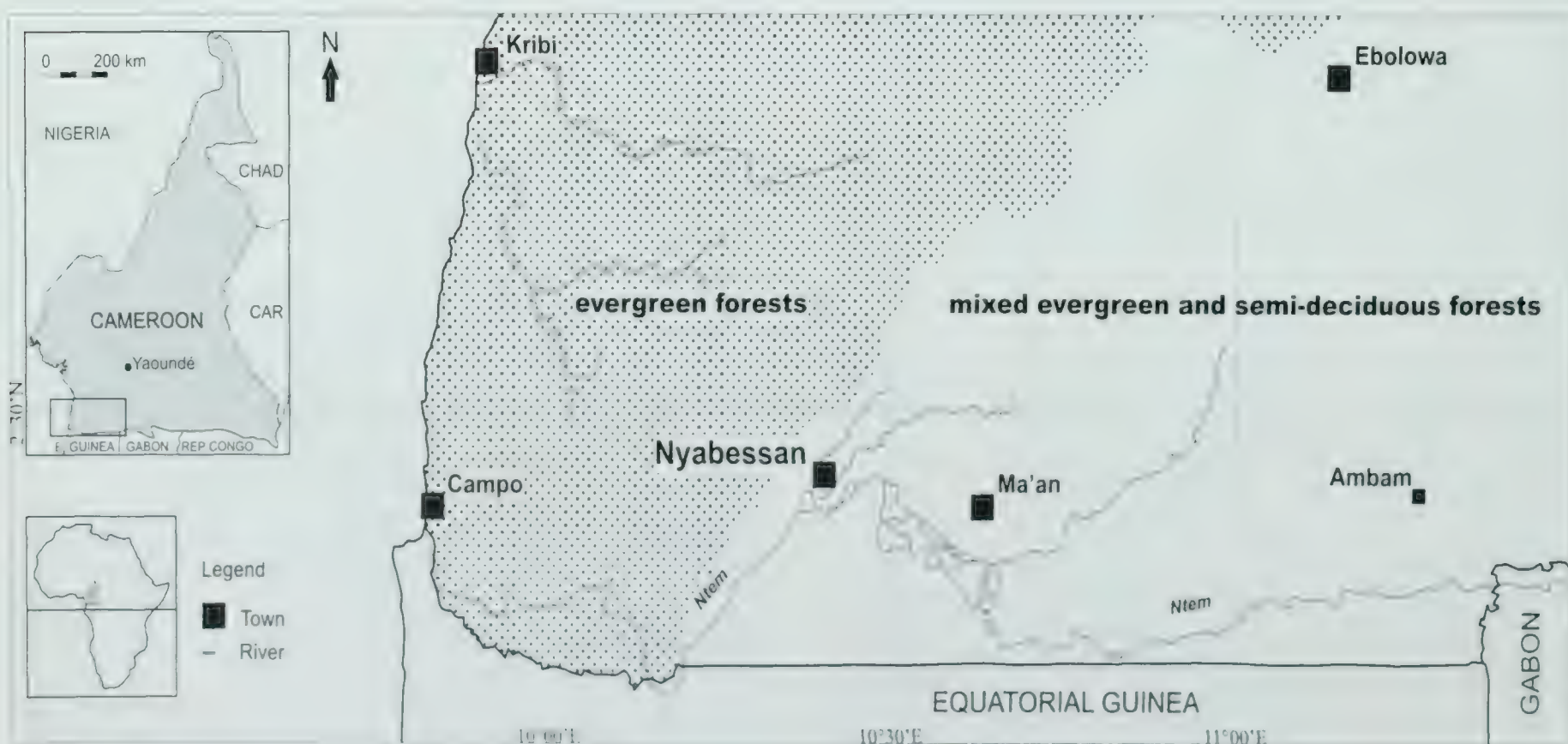


Figure 1 – Map of the study area.

The villages are situated along a decreasing precipitation gradient running 160 km from Campo on the coast (averaging 2797 mm per year) to Ambam in the hinterland (1697 mm per year). In the coast the various ethnic groups comprise the Mabea, the Yassa (mostly fishermen although some are farmers), and the Mvae, who are exclusively farmers. The density of Mvae people drops from the coast to the east where the Ntumu who are also farmers, form the dominant ethnic group.

The major part of the area is occupied by the Campo-Ma'an National Park, a protected area in which human activity is forbidden.

The area has four seasons: the long dry season (December to February), short rainy season (March to May), short dry season (June to August) and long rainy season (September to November). The climate of the area is equatorial, with an average temperature of 25°C.

Its bedrock is part of the Ntem formations made of metamorphic rocks comprising gneiss, quartzites, migmatites and charnokites dating from the Precambrian (Nougier 1979), about 2.5 billion years ago (Ngako 2006), and the features of the area's relief ranges from lowlands in the east to mountains of around 1000 m altitude in the west.

The soils are yellow ferralitic and derived from sedimentary rocks.

In the west, the primary vegetation consists of mature evergreen forest with *Saccoglottis gabonensis* and *Lophira alata*, which characterize the coastal aspect of the Atlantic forest with dominant Leguminosae-Caesalpinioideae (Letouzey 1985). From the coast into the hinterland, the vegetation changes due to decrease in both precipitation and human activities such as agriculture. In the east, beyond Nyabessan, population density is high. Semi-deciduous forest species grow together with those typical of evergreen forests. The percentage of evergreen forest species diminishes with distance from the sea whereas that of semi-deciduous forest elements increases. Despite this increase in semi-deciduous forest species towards the east, species characteristic of Atlantic forests such as *Rauvolfia macrophylla*, *Diospyros conocarpa* and *Hypodaphnis zenkeri* are still present.

Sampling

Plots of 20 × 20 m (i.e. covering an area of 0.04 ha each) were placed in the centre of fallows of different ages. In each plot, all plant species were recorded and a Braun-Blanquet index of cover-abundance was assigned to each species. Individuals of trees and shrubs measuring at least 5 cm diameter at breast height (dbh) were counted including, those of oil palm (*Elaeis guineensis*) and papaw (*Carica papaya*). For multi-stemmed individuals, each stem was counted and considered as an individual.

The percentage of canopy coverage was determined by making the projection of tree crowns onto the ground. Information related to the history of the fallows was obtained by interviewing their owners and the answers provided were considered as categorical variables. They include information on the previous vegetation, the number of farming cycles and the vegetation type surrounding the fallow.

The previous vegetation refers to the type of vegetation which was cleared before the last farming which was either a forest (mature or secondary) or a *Chromolaena* thicket. The number of farming cycles is the number of times the same plot had been converted to grow crop. The vegetation surrounding the fallows could be a forest (mature or secondary), a *Chromolaena* thicket or forest on one side and *Chromolaena* thicket on the other.

Data analysis

In order to assess the floristic diversity of the thickets, the Shannon diversity and the Pielou evenness indices were calculated. The Sørensen similarity coefficient (C_s) (Sørensen 1948) was also calculated to assess changes in species composition of fallows according to age. Given two samples, A and B, with a the total number of species in sample A, b that of B, and c the number of species common to samples A and B, C_s is equal to:

$$C_s = \frac{2 \times c}{a + b} \times 100$$

Cover abundance values of the floristic matrix were log transformed. Data were submitted to ordination and classification analysis using PC-ORD 5.19 (McCune & Mefford 2006). A nonmetric multidimensional scaling (NMS) ordination was carried out followed by a Cluster analysis to aid classification. The diagnostic species of each group were determined by performing an indicator species analysis (Dufrene & Legendre 1997), which determines the indicator value (IndVal) for each species in the various vegetation groups. The statistical significance of the indicator value was evaluated after running a Monte Carlo test with 1000 randomizations and by checking the p value at 0.05. Other statistical analyses (ANOVA) were done with PASW Statistics 18.0.

RESULTS

Location of the plots and variables controlling species composition

The vegetation group treated in this study is marked with a black contour line on the different ordinations graphs (fig. 2A–D) and belongs to group 7 (fig. 2A). Of the plots studied, 80% developed from fields established after clearing existing *Chromolaena* thickets (fig. 2B), whereas 17% were established in secondary forest and 3% in mature forest plots. The vegetation type around these thickets (fig. 2C) was a mature forest in 7% of the plots, a secondary forest in 27%, and a *Chromolaena* thicket in 56%, while 10% were bordered on one side by mature forest and on the other by a *Chromolaena* thicket. The number of agricultural cycles (fig. 2D) was 2 in 10% of the fallows, multiple in 80% and unknown for 10%.

Species diversity

The *Chromolaena* thickets studied comprise a set of thirty fallows aged from one to five years, with a mean age of 3 ± 1.05 years (table 1). Their flora comprises a total of 298 species belonging to 233 genera in 84 plant families. The species number per plot varies between thirteen and 72, with a

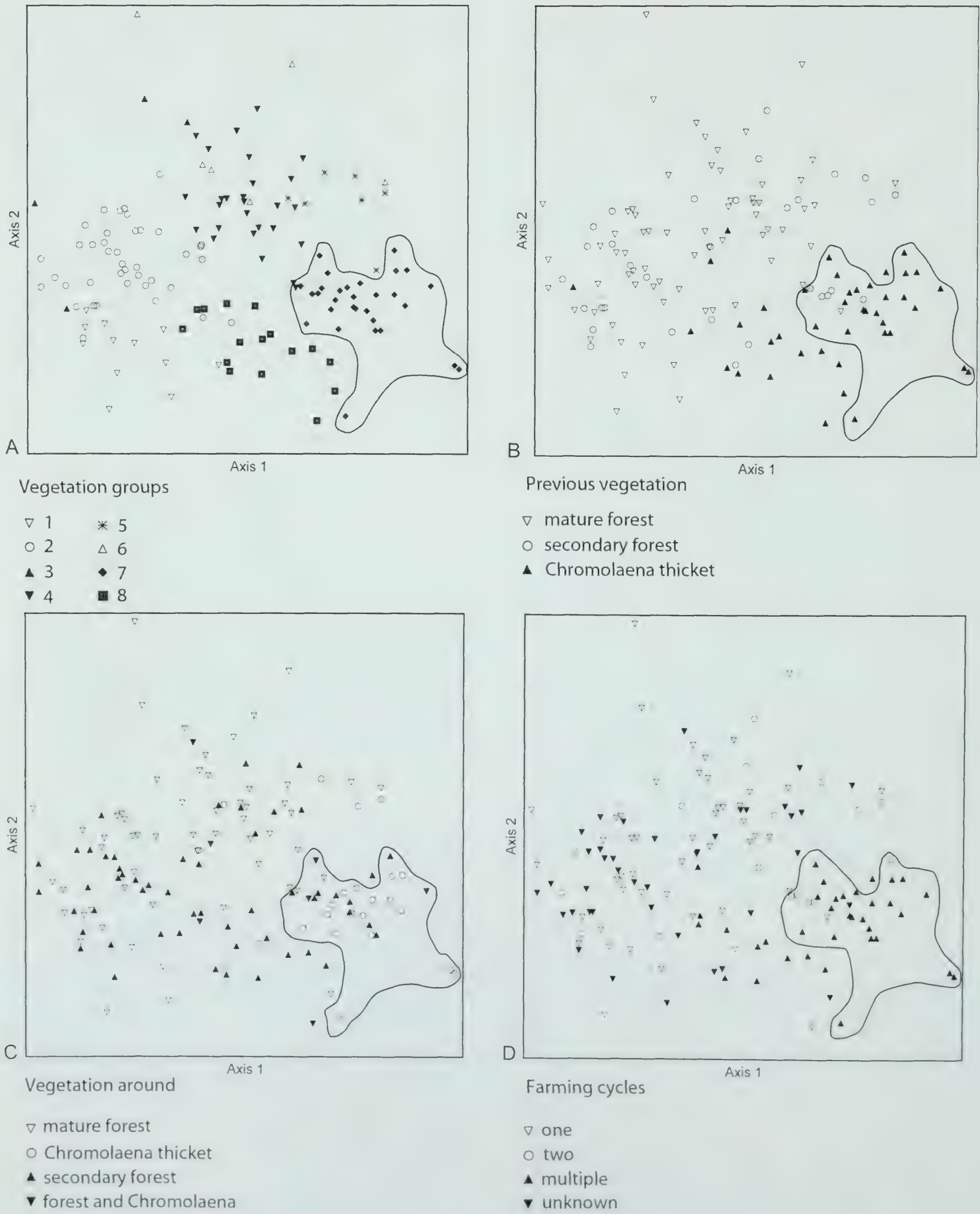


Figure 2 – Ordination results of the vegetation relevés: A, group 7 marked is the *Chromolaena* thickets; B, previous vegetation of the plots before the last clearance for farming; C, vegetation type around the plots; D, number of farming cycles of in the plots before clearance.

Table 1 – Statistics of age, diversity indices and canopy closure.
Min: Minimum; Max: Maximum; Std Dev: Standard Deviation.

	Min	Max	Mean	Std Dev
Age	1	5	3	1.05
Number of species	13	72	44.81	14.71
Shannon index	1.32	4.17	2.84	0.6
Pielou's evenness	0.47	0.95	0.7	0.10
Canopy closure	0	30	3.88	7.86

mean of 44.81 ± 14.17 species per plot. The plot with the lowest values of species richness (13 and 24) were found in fallows 137 and 138, both established on sandy soils in the coastal area, mostly constituted of coarse grains of sand. In contrast, the plot with the highest value (72 species) was observed in fallow 91, established on silty soil at Nyabessan in the inland.

Some families are represented by more species than others, as it is the case of Leguminosae, which ranks first with 31 species (10.41%) and 22 genera (9.44%). They are followed by Rubiaceae, Euphorbiaceae and Asteraceae represented each by at least ten genera (more than 4%), all three of which also have high species diversity. Together with Poaceae and Apocynaceae, they represent the most diverse families, with at least ten species each.

Of the genera with more than two species, *Bertiera* ranks first with five species, followed by *Cissus*, *Cyperus*, *Dioscorea*, *Milletia* and *Palisota*, each with four species. While some genera such as *Cissus*, *Dioscorea*, *Costus* and *Macaranga* are related to disturbed forest areas, others including *Cola*, *Milletia* and *Treculia* grow in mature forests.

Of the 298 species recorded overall, 78% are present in less than six plots (20% of the relevés). They have a low frequency and were assigned a presence degree of I. The frequency histogram (fig. 3) shows that just a few species are present in the majority of fallows. Only *Alchornea cordifolia*, *Chromolaena odorata*, *Desmodium adscendens* and *Ipomoea involucrata* have a relative frequency of more than 80%, which corresponds to a presence degree of V.

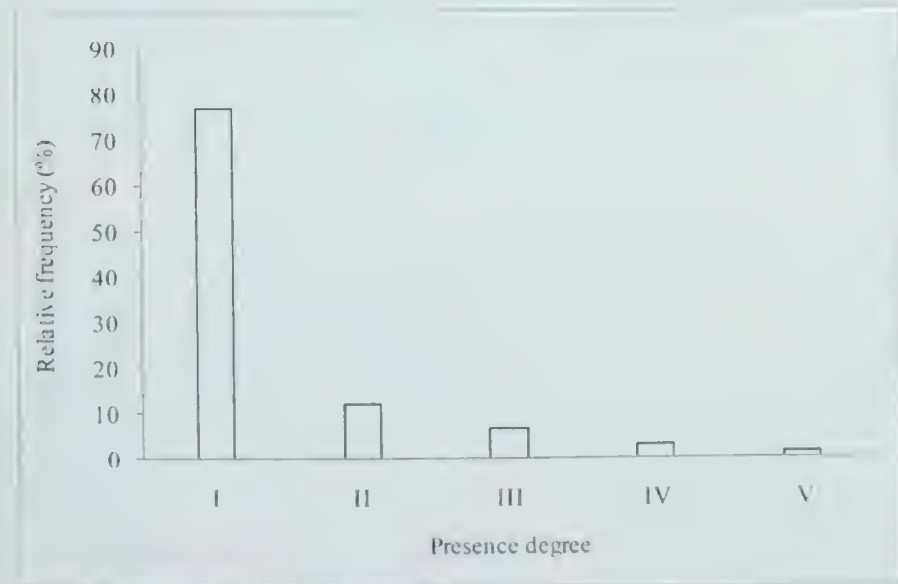


Figure 3 – Presence degree of plant species in the *Chromolaena* thickets.

Table 2 – Key species with their presence degree (P. Deg.), indicator values (IndVal) and p value of Monte Carlo test.

Species	P. Deg.	IndVal	p value
<i>Chromolaena odorata</i> (L.) R.M.King & H.Rob.	V	47	0.001
<i>Desmodium adscendens</i> (Sw.) DC.	IV	20	0.212
<i>Alchornea cordifolia</i> (Schumach.) Müll.Arg.	IV	22	0.434
<i>Phyllanthus amarus</i> Schumach.	IV	29	0.01
<i>Asystasia gangetica</i> (L.) T.Anderson	IV	31	0.006
<i>Pteridium aquilinum</i> (L.) Kuhn	II	21	0.053
<i>Stachytarpheta cayennensis</i> (Rich.) Vahl	III	32	0.004
<i>Fimbristylis hispidula</i> Kunth	II	28	0.022
<i>Ageratum conyzoides</i> L.	II	20	0.074
<i>Axonopus compressus</i> (Sw.) P.Beauv.	III	21	0.03

Chromolaena is the species with the highest indicator value and the lowest p values (table 2), and is the main characteristic species of this plant community. Despite their high relative frequency and presence degree, *Ageratum conyzoides*, *Alchornea cordifolia* and *Desmodium adscendens* are not diagnostic species of this community, as their p values are higher than 0.05.

Structure

In thickets *Chromolaena* can reach 5 m in height, forming a canopy below which herbs and seedlings of forest trees are present. Weeds and ruderal species are often mixed with remnants of food crops such as cocoyam (*Xanthosoma sagittifolium*) and groundnut (*Arachis hypogea*). The thicket is so dense that it is difficult for wind-dispersed seeds to pass through and reach the soil of the fallows.

There is no true tree layer due, to the poverty of these life form both in terms of species and individuals. The canopy closure percentage (table 1) of the thickets is not higher than 30% and in a majority of the plots (63%) it is zero.

In these fallows, 274 tree and shrub individuals representing 41 species were recorded for a total average basal area of 2.5 m² per ha. The most represented dbh classes (fig. 4) are those between 5 and 20 cm which correspond to the lower strata of Letouzey (1982) and comprise 96.35% of the total individuals recorded in the fallows. The most abundant species are the forest pioneers *Anthocleista schweinfurthii*, *Macaranga hurifolia* and *Musanga cecropioides*. The medium tree layer had only five species and eight individuals of dbh between 20 and 25 cm. *Elaeis guineensis* the oil palm was the only species present in the upper layer with two individuals of 50 and 62 cm dbh.

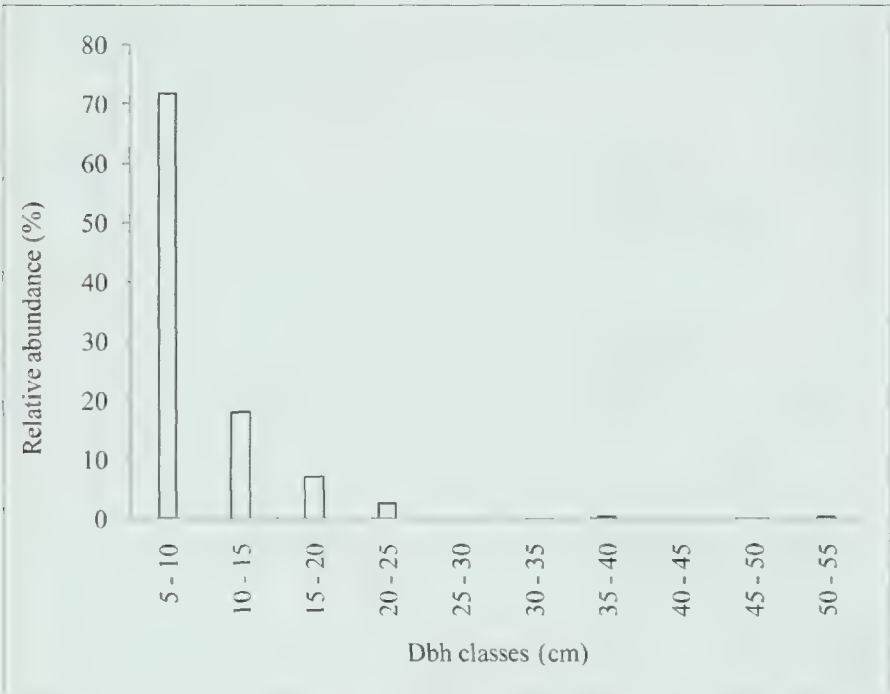


Figure 4 – Dbh classes of trees and shrubs in the thickets.

Dynamics

The values of the Sørensen similarity coefficient according to fallow age are presented in table 3. The highest values are observed after one year of abandonment. After this period almost all thicket species are already present in the fallows.

After abandonment, the field is invaded by herbaceous species and young individuals of *Chromolaena*. Seedling of some forest tree species can also be found growing in these fallows. Most of the herbs are annuals and after their disappearance, they are often replaced by new individuals of *Chromolaena* which contribute to the persistence of the thicket.

After two years, the canopy of *Chromolaena* is already in place and its height can reach 4 m or more.

However, under and around the trees which were left behind by the farmer during clearing, stems of *Chromolaena* weaken and die. At the same time, the development of saplings of forest species which was low under the canopy of *Chromolaena*, is stimulated by exposure to light due to thinning and disappearance of the thicket. The situation is the same for the thickets that were bordered by forest. A centripetal forest recovery takes place.

DISCUSSION

Farming system and structure of the thickets

Shortening fallow length and multiple farming cycles highly influence forest recovery. Frequent and regular clearings of

Table 3 – Sørensen similarity coefficient between fallows of different ages.

	1 year	2 years	3 years	4 years	5 years
1 year	100				
2 years	58.55	100			
3 years	90.24	54.81	100		
4 years	62.06	52.96	62.16	100	
5 years	58.37	43.68	45.64	51.50	100

a given plot reduce plant residuals which play an important role in forest recovery in tropical regions (Alexandre 1989, Aide et al. 1995, Chazdon 2003). The necessary conditions for normal asuccession cycle are regularly modified if not curtailed by this practice. The four different pathways of forest regeneration represented by seedlings, sprouts, soil seed bank and seed dispersal (Uhl et al. 1990) are massively constrained by multiple clearing, fire and weeding. Although fire increases soil fertility in the short term by releasing nutrients from plant material (Ewel et al. 1981), its regular and frequent use affects the establishment of other species in the fallows (Uhl & Buschbacher 1985), soil properties (Certini 2005), and competition (Nepstad et al. 1990), and at the same time eliminates part of the soil seed bank (Uhl 1987). This practice is detrimental to colonization of the fallow by seeds of forest species during recovery after shifting cultivation. Our results are consistent with those of Guarigata & Ostertag (2001), Uriarte et al. (2004), and Chazdon et al. (2006) according to whom forest recovery depends on the disturbance regime, its intensity and frequency.

With a basal area of 2.5 m² per ha, the value in the plots studied is low when compared to other fallows studied elsewhere in the tropics. In Venezuela, Uhl (1987) obtained a basal area of 4 m² and 7m² per ha, respectively after three and five years of abandonment in a plot that had been farmed once after cutting down an old-growth forest. In the Dominican Republic, Riviera et al. (2000) found a basal area of 5.5 m² per ha in pastures not older than five years. The difference between our values from Cameroon and those from other areas lies in the use of multiple farming cycles. Frequently converting the same plot into field crop within a short period does not give the regeneration mechanisms (Uhl 1987) enough time to speed up forest recovery. Successive clearing and burning alter not only plant residuals but also part of the seed bank in the soil (Chazdon 2003). The weeding that follows planting is a step during which the farmer eliminates not only weeds, but also sprouts and coppices of forest tree species. In other words, this farming practice alters above ground biomass (James 1984, Bellingham & Sparrow 2000, Finegan & Delgado 2000), which is one important factor in forest succession. This explains the rarity of trees in the plots we studied and the few trees that were observed resembled the shrubs in having low dbh values. These results are consistent with those of Uhl et al. (1988), Aide & Cavellier (1994), Aide et al. (1995), Guariguata et al. (1997), and Riviera et al. (2000), all of which show that land use history of fallows explains the slow rate or delay in forest recovery.

Floristic composition and species diversity

Southern Cameroon is part of the Congo basin, which belongs to the Guineo-Congolian centre of endemism (White 1983), and forms part of the Lower Guinea forest refugia (Maley 1987, Linder 2001), which is rich in endemic species. The study area exhibits the predominance of Leguminosae-Caesalpinioideae, a variant of the Atlantic forest of Cameroon according to Letouzey (1985). White (1983) characterized this centre of endemism by the presence of certain families of large trees such as Leguminosae (Mimosoideae, Caesalpinioideae), Guttiferae, Moraceae, Myristicaceae, and

Sapotaceae, all of which are present in our plots. The flora of the thickets we studied reflects that of the entire phytogeographical region.

The dominance of *Chromolaena* shows that growing conditions are quite homogeneous in the fallows and consequently, species richness is low. The presence of thickets hampers the growth of other species and explains why many species are rare in the plots. In addition, the L shape of this histogram is typical of homogeneous plant communities (Emberger 1954), reflecting a species richness pattern in which few species are dominant.

Zapfack et al. (2002) studied the impact of land conversion on plant diversity in different land use systems in southern Cameroon and recorded 142 species in *Chromolaena* plots, considerably lower than the 298 species recorded in the current study. The difference lies with the sampling method: Zapfack et al. (2002) took into consideration only woody individuals of 2.5 cm dbh, and thus did not include species of other life forms.

With regard to the observed variation in species richness from 13 to 72 species per plot, low values are correlated with the acidic nature of sandy soils on which some of the plots were established. The high content of coarse sand lowers their nutrient retention capacity and increases permeability. Many species cannot develop on these soils which explains their low species richness.

Dynamics

One year after abandonment is sufficient time for species recruitment, as shown by the fact that beyond this period, values of Sørensen similarity coefficient are high. This is the length of time necessary for the initial floristic composition (Egler 1954) to be put in place from both the soil seed bank and input of diaspores, especially of wind dispersed shade tolerant species. Once the thicket is formed, the growth of saplings of forest species is hampered, especially of those that cannot tolerate shade.

The vegetation around the thickets has an overwhelming influence on their dynamics. It provides fallows with input of propagules capable of enriching the flora of these fallows, and constitutes what Alexandre (1982) referred to in French as “advectif potentiel” (potential advective). Since the surrounding vegetation of the fallows consists in most cases of *Chromolaena* stands, seeds mostly of this plant will reach the fallows, resulting in the persistence of this vegetation type, which can last up to twenty years (Kushwaha et al. 1981), as is the case in northern India. However, in plots where the surrounding vegetation was a forest, shade created by trees growing around the thickets results in weakness and senescence of *Chromolaena* stems. The resulting openings allow light to reach the soil and give the opportunity to individuals of forest tree species that were in standby under the canopy of *Chromolaena* to develop. *Chromolaena odorata* is a light demanding species that for its normal growth and development does not tolerate any obstacle in its environment. Once a tree protrudes from the thicket, its shade triggers the death of *Chromolaena* stems. Since the plots we examined were poor in trees, this is an advantage for *Chromolaena*. The situation is exactly the same with the trees that were left behind

by farmers during clearing as their shade is responsible of the gradual disappearance of the thicket under and around them.

The environment created by *Chromolaena* thickets does not favour the establishment of new species in the fallow. The persistence of the thicket acts as a shield that limits the deposition of external propagules. It causes a delay in forest recovery and can explain low species richness and basal area. During succession, the mechanism of species replacement in *Chromolaena* thickets follows the inhibition model of Connell & Slatyer (1977).

CONCLUSION

Our results confirm the idea of Chazdon (2003) that forest recovery depends on the type, frequency and duration of disturbance. The status of *Chromolaena*, either as a weed or a fallow species remains open to debate. Plant ecologists regard it as fallow plant responsible for the delay in forest recovery, while agronomists consider it to be a good source of natural fertilizer. Sound management of this plant, considered as a weed, implies improvement of farming practices since *Chromolaena* is partially responsible for the delay of forest regeneration. Given that farmers prefer to cultivate *Chromolaena* thickets rather than often clearing mature forest and that *Chromolaena* improves soil fertility, future cultivation of these thickets could be advisable in order to reduce the rate of deforestation and the resulting threats to endangered species.

ACKNOWLEDGEMENTS

The authors highly thank the German Ministry of Foreign Affairs (BMZ) which entirely sponsored this work. The authors express their gratitude to Mrs. Barbara Voss who improved the quality of ordination graphs and to Dick Byer who corrected the English. The General Manager and President of the Board of the Institute for Agricultural Research for Development (IRAD), the mother institution of the National Herbarium of Cameroon are thanked for having issued mission orders to the corresponding author whenever he flew to Frankfurt in the framework of this research.

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Manuscript received 15 Nov. 2010; accepted in revised version 28 Mar. 2012.

Communicating Editor: Porter P. Lowry II.



Impact of *Sericostachys scandens* on forest regeneration in the Kahuzi-Biega National Park, D.R.Congo

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Background and aims – *Sericostachys scandens* (Amaranthaceae), an indigenous liana in Kahuzi-Biega National Park (KBNP, D.R.Congo), has been spreading strongly in montane forests for about ten years. We have tried to assess the consequences of this expansion on forest regeneration.

Methods – We carried out an inventory of tree individuals (≥ 1 m in height) growing in 33 gaps in the montane forests located between 2083 and 2424 m altitude.

Based on three age classes of gaps (1996, 2000 and 2004), the inventory was carried out in the plot of 10 m $\times$ 10 m, in sites invaded and non invaded by *Sericostachys scandens*. The *EstimateS* software was used to calculate the expected number of plant species in order to plot cumulative species richness curves. The relative frequency of species and the Simpson index of diversity were calculated for the two types of vegetation (invaded vs. not-invaded).

Results – Irrespective of gap age, cumulative curves obtained from the expected number of plant species show that plots without *Sericostachys scandens* are richer in species than those with the liana. The values of relative frequency of species, and Simpson index obtained are highest in forest gaps without the liana. The impact of the liana is larger in more recent gaps.

Conclusions – The results of this research show that *Sericostachys scandens* has a negative impact on tree species richness in forest gaps of KBNP.

Key words – *Sericostachys scandens*, forest regeneration, montane forest, impacts, gaps, Kahuzi-Biega National Park.

INTRODUCTION

Forest regeneration is the renewal or restoration of the forest after some openings in the forest canopy was formed, caused by disturbances such as tree fall. During this process, seeds stored in the ground will take advantage of increased light to germinate and existing seedlings will further develop (Hubbell & Foster 1986, Hubbell et al. 1999, Kukkonen et al. 2008). According to Denslow (1995), the fall of trees influences the species richness and density in forest communities. Gap formation provides different micro-environmental conditions (e.g. higher solar radiation, temperature and evaporation at soil surfaces, and lower air moisture and incidence of pathogens), compared to the ones of an undisturbed forest (Brokaw 1985). These are important to maintain dynamic processes in the forest. According to ecologists, forest regeneration is defined as the whole dynamic process leading to the reconstruction of the canopy (Alexandre 1989). In general, species richness may recover rapidly during regeneration

(Hooper et al. 2004). The gap dynamics is described as an important factor in the restoration of plant community structure by increasing environmental space heterogeneity, allowing forest canopy species to grow (Hartshorn 1978, Whitmore 1978, 1988, Denslow 1985, 1987, Ashton 1990, Carvalho et al. 2000). It is also reported that lianas are thriving in areas of abundant light (Baars et al. 1998).

Lianas are plants that germinate on the forest ground and grow, at least for part of their life by winding around, leaning on, anchoring or adhering to other plants (Jongkind & Hawthorne 2005). Lianas are important for the ecology of tropical forests in several ways. They can influence forest dynamics by slowing tree growth rate (Putz 1984; Bongers et al. 2002; Schnitzer & Bongers 2002), by increasing tree mortality (Clark & Clark 1990), and by slowing the rate of forest regeneration in gaps where they cover the ground (Putz et al. 1984; Schnitzer et al. 2000). They can also have a direct negative effect on tree fecundity (Stevens 1987). Chatelain et

al. (2004) and Bongers et al. (2005) identified the abundance of lianas as one of the characteristics of forests disturbed by agriculture (Laurance et al. 2001).

Kahuzi-Biega National Park (KBNP) is an area of primary tropical forest dominated by two spectacular extinct volcanoes, Kahuzi and Biega and is situated in eastern part of the D.R.Congo. Due to conflicts in the region over the last two decades, the park suffered from many anthropic disturbances. This is why, in 2006, the United Nations Educational, Scientific and Cultural Organization (UNESCO) classified the park as a world heritage in danger (Mubalama & Bashige 2006).

In the last decade, managers of the Park have drawn attention to the rapid expansion of the native liana *Sericostachys scandens* Gilg & Lopr. (Amaranthaceae) (Iyomi 2005). As this species is apparently spreading in gaps and disturbed sites, it might conceivably affect negatively forest regeneration. In the present paper, we want to test this hypothesis. To that end, we examine tree species richness in gaps of various ages, either invaded or not by *Sericostachys*. In particular, we test i) if tree species richness and diversity is lower in gaps

invaded by *Sericostachys scandens*, ii) if some tree species have lower abundance in invaded gaps and iii) if these differences are influenced by gap age.

STUDY AREA

The study was carried out in the KBNP (latitude 1°36'–2°37'S and longitude 27°33'–28°46'E; fig. 1), located in the western dorsal part of Lake Kivu in the D.R.Congo (Mühlenberg et al. 1994). The park covers 6000 km² and includes lowland forests (5400 km²) and montane forests (600 km²). These ones are found between 1800 and 3308 m of altitude.

The Kahuzi Biega vegetation comprises mountainous area colonized by bamboo forests belt (37%), dicotyledonous primary forests (28%), and secondary forests (20%), swamps (7%) covered by *Cyperus* sp. (Goodall 1977; Yumoto et al. 1994). All other types of vegetation represent 8% of the study area.

The present study deals with both secondary and primary forests occurring at an altitude ranging from 2083 to 2621 m.

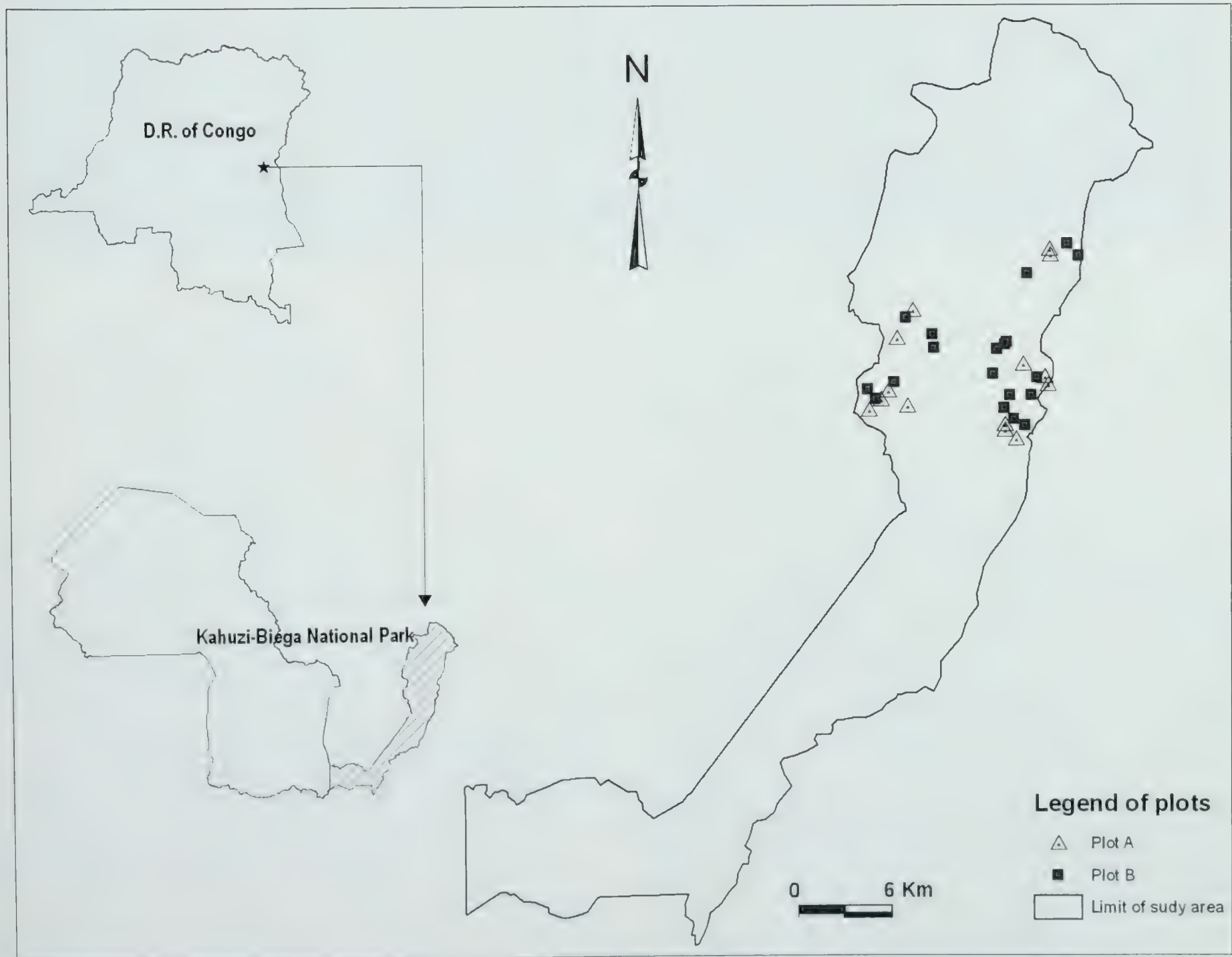


Figure 1 Study area within the Kahuzi-Biega National Park, D.R.Congo. Plot A (invaded by *Sericostachys scandens*) and plot B (not-invaded by liana).



Figure 2 – Gap invaded by *Sericostachys scandens* (plots B).

METHODS

Thirty-three gaps were located by the monitoring team of the Park in different sites (Tshivanga, Mugaba, Madiriri and Cibati) in 2008, time during which the data analysed in this study were collected. The sizes of the gaps were variable, but generally larger than 300 m². Out of thirty-three forest gaps, eighteen were dominated by *Sericostachys scandens* (plot B; fig. 2) whereas this liana was completely missing in the fifteen other plots (plot A). *Sericostachys scandens* is a climber heliophilous. This liana is often dominant in the gaps as it is densely branched and produces many leaves.

Three gap age classes were distinguished to evaluate the impact of *Sericostachys scandens* on forest regeneration: 1996 (old gaps), 2000 (intermediate) and 2004 (young). Secondly, the two groups were examined separately, without considering the date of gaps creation.

In each gap, we used Lima & Moura (2008) protocol and established a sample plot of 10 m × 10 m in each gap. We listed all tree species ≥ 1m height growing in these gaps from 1996 to 2004 in KBNP. All individuals of tree species growing in the plot were counted and identified.

The *EstimateS* software package (Colwell 2005) was used to analyze the data. This allowed us to generate the expected number of species, as done by Denslow (1995) in his study on floristic diversity disturbance in tropical humid forests. Data

generated were used to plot cumulative curves, in order to assess species richness among the two different sampled plot vegetation types. The expected number of plant species $E(Sn)$ in a sample of size n is given by the following equation:

$$E(Sn) = \sum_{i=1}^s \left[1 - \frac{\binom{N-N_i}{n}}{\binom{N}{n}} \right]$$

Where N is the total number of individuals of the species in a sample, s the total number of species and N_i the number of individuals of the species number i .

Based on the relative frequency (RF_{kj}), we compared the floristic composition of tree species in gaps dominated by *Sericostachys scandens* with the situation in gaps without this liana. The T-test has been used in order to assess differences in species frequency between plots dominated by the liana and plots where *Sericostachys.scandens* is absent. The relative frequency is useful, as it allows comparison between two distributions of frequencies from samples of different sizes. It varies from 0 to 100. Molina-Freaner & Tinoco-Ojanguren (1997) also used the relative frequency to compare the abundance of lianas between sites.

McCune & Grace (2002) described the method for calculating the relative frequency. The relative frequency (RF_{kj}) is computed after transformation of the matrix of abundance in presence-absence matrix ($b_{ij} = a_{ij}^0$):

Table 1 – Comparison of the floristic composition between the plots invaded by *Sericostachys scandens* and non-invaded plots.
All gap age classes were pooled. Plot A = non-invaded plot (number of plots = 15; number of sites = 4); Plot B = plot invaded (number of plots = 18; number of sites = 4). Relative frequency = percentage of gaps in which the species is found; t-test; p-Value for relative frequency: NS = no significant difference, * = significant difference.

Species	Family	Relative frequency		p-Value
		Plot B	Plot A	
<i>Chrysophyllum gorungosanum</i> Engl.	Sapotaceae	-	27	*
<i>Macaranga neomildbraediana</i> Lebrun	Euphorbiaceae	28	53	NS
<i>Neoboutonia macrocalyx</i> Pax	Euphorbiaceae	30	52	NS
<i>Tabernaemontana stapfiana</i> Britten	Apocynaceae	6	33	NS
<i>Dombeya torrida</i> (J.F.Gmel.) Bamps	Sterculiaceae	28	20	NS
<i>Albizia gummifera</i> (J.F.Gmel.) C.A.Sm.	Fabaceae	11	20	NS
<i>Cassipourea louisii</i> Liben	Rhizophoraceae	6	27	NS
<i>Sapium ellipticum</i> Hochst. ex Krauss	Euphorbiaceae	11	20	NS
<i>Symphonia globulifera</i> L.f.	Clusiaceae	-	13	NS
<i>Syzygium guineense</i> (Willd.) DC.	Myrtaceae	11	13	NS
<i>Newtonia buchananii</i> (Baker) Gibl. & Bout.	Fabaceae	-	13	NS
<i>Polyscias fulva</i> (Hiern) Harms	Araliaceae	28	13	NS
<i>Xymalos monospora</i> (Harv.) Baill.	Monimiaceae	-	13	NS
<i>Bridelia brideliifolia</i> (Pax) Fedde	Euphorbiaceae	11	13	NS
<i>Alangium chinense</i> (Lour.) Harms	Alangiaceae	-	13	NS
<i>Grewia mildbraedii</i> Burret	Tiliaceae	-	13	NS
<i>Myrianthus holstii</i> Engl.	Cecropiaceae	11	7	NS
<i>Syzygium rowlandii</i> Sprague	Myrtaceae	-	7	NS
<i>Drypetes</i> sp.	Euphorbiaceae	6	7	NS
<i>Strombosia scheffleri</i> Engl.	Olacaceae	6	7	NS
<i>Carapa grandiflora</i> Sprague	Meliaceae	6	7	NS
<i>Cassipourea gummiflua</i> Tul.	Rhizophoraceae	-	7	NS
<i>Maerua bussei</i> (Gilg & Bened.) R.Wilczek	Capparidaceae	-	7	NS
<i>Maesa lanceolata</i> Forssk.	Myrsinaceae	6	7	NS
<i>Pleiocarpa pycnantha</i> (K.Schum.) Stapf	Apocynaceae	6	7	NS
<i>Zanthoxylum gillettii</i> (De Wild.) P.G.Waterman	Rutaceae	-	7	NS
<i>Bersama abyssinica</i> Fres.	Melanthaceae	6	-	NS
<i>Millettia dura</i> Dunn	Fabaceae	6	-	NS
<i>Nuxia floribunda</i> Benth.	Loganiaceae	6	-	NS

$$RF_{jk} = \frac{\sum_{i=1}^{n_k} b_{ijk}}{n_k}$$

Where a_{ijk} = abundance of species j in sample unit i of group k and n_k = number of sample units in group k .

Species diversity has been computed using the Simpson's Index (D). This index represents the likelihood that two randomly chosen trees belong to the same species (MacCune & Grace 2002; Grall & Hily 2003):

$$D = \sum \left(\frac{N_i(N_i - 1)}{N(N - 1)} \right)$$

Where N_i : number of individuals of a given species and N : total number of individuals.

This index varies from 0 to 1: 0 indicates the maximum diversity and 1 the minimum diversity. But in this case, we

used the Simpson Index of diversity represented by $1 - D$ in order to get more intuitive value (Grall & Hily 2003). It should be noted that the Simpson's Index gives more weight to abundant species than to rare species. The addition of rare species in a sample does not substantially alter the value of Simpson's Index.

RESULTS

Species richness

We have listed 29 tree species belonging to 27 genera and twenty families, both in gaps colonized by *Sericostachys scandens* and in gaps that were not invaded. Only three species (*Bersama abyssinica*, *Millettia dura*, and *Nuxia floribunda*) were absent in plots without the liana whereas ten species were absent from the plots colonized by *Sericostachys scandens*, i.e. *Alangium chinense*, *Cassipourea gummiflua*, *Chrysophyllum gorungosanum*, *Grewia mildbraedii*, *Mae-*

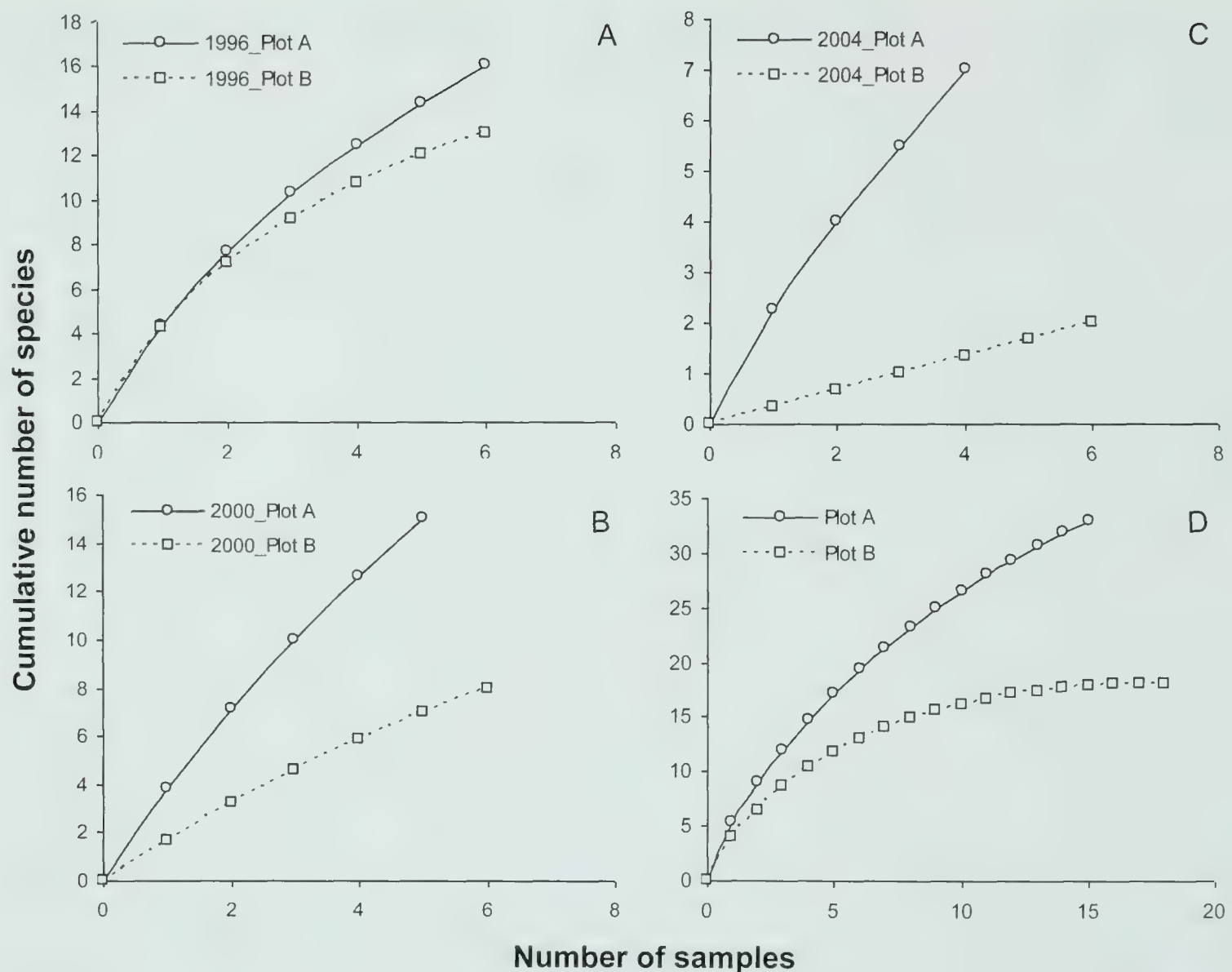


Figure 3 – Tree species richness cumulative curves in gaps of three age classes A, B, C (1996, 2000, and 2004) and the global curve D represents the plots A (not invaded by *Sericostachys scandens*) and B (invaded).

rua bussei, *Newtonia buchananii*, *Symphonia globulifera*, *Syzygium rowlandii*, *Xymalos monospora*, and *Zanthoxylum gillettii*.

Based on age classes, cumulative curves obtained from the expected number of species in samples were used to compare the species richness between the plots dominated by *Sericostachys scandens* liana and the plots where this liana species was not found, first according to the age class of the gaps (fig. 3A–C), and then globally (fig. 3D).

The cumulative curves representing the three age classes (fig. 3A–C) show that species richness was systematically higher in plots where *Sericostachys scandens* was absent. Interestingly, species richness seems also correlated to the gap's age: in oldest gaps (1996, fig. 3A), the difference between both cumulative numbers of species (plot A and plot B) is less significant than the difference seen in younger gaps (fig. 3B & C).

The global situation of species richness in gaps created from 1996 to 2004 is illustrated in figure 3D. The cumulative curve of gaps where *Sericostachys scandens* was absent is higher than those of gaps where *Sericostachys scandens* was present.

Relative frequency and Simpson Index

In this part, we compared floristic composition between the plots invaded by *Sericostachys scandens* in relation to those

without the liana in general, and following their age classes. Plant species lists are given in tables 1, 2, 3 and 4; from these lists, relative frequency has been computed. In table 1, the plots invaded by the liana and the ones without this species were compared globally. Among 29 species recorded in both invaded and non-invaded plots, 26 are represented in plots non-invaded, and nineteen species are found in plots invaded by the liana. In the plots without *Sericostachys scandens*, *Chrysophyllum gorungosanum* has high values of relative frequency (27%) while it is absent in plots with the liana ($p = 0.041$).

Based on gap class ages, in the young gaps invaded by *Sericostachys scandens* (table 2), only two species namely *Neoboutonia macrocalyx* and *Dombeya torrida* were found. On the other hand, these species are confined only to small number of plots being invaded by *Sericostachys scandens*. *Macaranga neomildbraediana*, *Sapium ellipticum* and *Neoboutonia macrocalyx* are present in large number of plots not invaded by the liana *Sericostachys scandens* (50%; 50%; 75%, respectively). Their relative frequencies are significantly higher in these plots than in plots invaded ($p = 0.029$; $p = 0.029$; $p = 0.038$, respectively).

For gaps formed in 2000 (table 3), two species have significantly higher values of relative frequency in plots without *Sericostachys scandens* than in those invaded by the liana ($p = 0.024$ each). These include *Tabernaemontana stapfiana* represented in 60% of non-invaded plots, but not represented

Table 2 – Comparison of the floristic composition between the plots invaded by *Sericostachys scandens* and non-invaded plots. Gap age: 2004. Plot A = non-invaded plot (number of plots = 4; number of sites = 3); Plot B = plot invaded (number of plots = 6; number of sites = 2). Relative frequency = percentage of gaps in which the species is found; t-test; p-Value for relative frequency: NS = no significant difference, * = significant difference.

Species	Relative frequency		p-Value
	Plot B	Plot A	
<i>Macaranga neomildbraediana</i>	-	50	*
<i>Neoboutonia macrocalyx</i>	17	75	*
<i>Sapium ellipticum</i>	-	50	*
<i>Albizia gummifera</i>	-	25	NS
<i>Syzygium guineense</i>	-	25	NS
<i>Tabernaemontana stapfiana</i>	-	25	NS
<i>Cassipourea gummiflua</i>	-	25	NS
<i>Dombeya torrida</i>	17	20	NS
<i>Polyscias fulva</i>	-	25	NS

Table 3 – Comparison of the floristic composition between the plots invaded by *Sericostachys scandens* and the non-invaded plots. Gap age: 2000. Plot A = non-invaded plot (number of plots = 5; number of sites = 2); Plot B = plot invaded (number of plots = 6; number of sites = 3). Relative frequency = percentage of gaps in which the species is found; t-test; p-Value for relative frequency: NS = no significant difference, * = significant difference.

Species	Relative frequency		p-Value
	Plot B	Plot A	
<i>Neoboutonia macrocalyx</i>	33	60	*
<i>Tabernaemontana stapfiana</i>	-	60	*
<i>Cassipourea louisii</i>	17	40	NS
<i>Chrysophyllum gorungosanum</i>	-	20	NS
<i>Dombeya torrida</i>	17	20	NS
<i>Macaranga neomildbraediana</i>	-	20	NS
<i>Myrianthus holstii</i>	17	20	NS
<i>Syzygium guineense</i>	-	20	NS
<i>Sapium ellipticum</i>	-	20	NS
<i>Strombosia scheffleri</i>	-	20	NS
<i>Albizia gummifera</i>	-	20	NS
<i>Grewia mildbraedii</i>	-	20	NS
<i>Newtonia buchananii</i>	-	20	NS
<i>Pleiocarpa pycnantha</i>	17	20	NS
<i>Xymalos monospora</i>	-	20	NS
<i>Carapa grandiflora</i>	17	20	NS
<i>Maesa lanceolata</i>	17	-	NS
<i>Polyscias fulva</i>	33	-	NS

in plots invaded, and *Neoboutonia macrocalyx* represented in 60% of non-invaded plots against 30% in plots invaded. Among eighteen species inventoried in this class of age, two are not present in the plots without the liana (*Maesa lanceolata* and *Polyscias fulva*). Conversely, in gaps invaded, ten species are lacking (*Chrysophyllum gorungosana*, *Syzygium*

Table 4 – Comparison of the floristic composition between the plots invaded by *Sericostachys scandens* and those which are not invaded. Gap age: 1996. Plot A = non-invaded plot (number of plots = 6; number of sites = 2); Plot B = plot invaded (number of plots = 6; number of sites = 2). Relative frequency = percentage of gaps in which the species is found; p-Value for relative frequency: NS = no significant difference, * = significant difference.

Species	Relative frequency		p-Value
	Plot B	Plot A	
<i>Chrysophyllum gorungosanum</i>	-	50	*
<i>Macaranga neomildbraediana</i>	83	83	NS
<i>Neoboutonia macrocalyx</i>	17	50	NS
<i>Symphonia globulifera</i>	-	33	NS
<i>Dombeya torrida</i>	50	17	NS
<i>Bridelia brideliifolia</i>	33	33	NS
<i>Cassipourea gummiflua</i>	-	33	NS
<i>Newtonia buchananii</i>	-	17	NS
<i>Alangium chinense</i>	-	33	NS
<i>Polyscias fulva</i>	50	17	NS
<i>Syzygium rowlandii</i>	-	17	NS
<i>Xymalos monospora</i>	-	17	NS
<i>Drypetes</i> sp.	17	17	NS
<i>Albizia gummifera</i>	33	17	NS
<i>Tabernaemontana stapfiana</i>	17	17	NS
<i>Carapa grandiflora</i>	-	17	NS
<i>Grewia mildbraedii</i>	-	17	NS
<i>Maerua bussei</i>	-	17	NS
<i>Maesa lanceolata</i>	-	17	NS
<i>Zanthoxylum gillettii</i>	-	17	NS
<i>Syzygium guineense</i>	33	17	NS
<i>Sapium ellipticum</i>	33	17	NS
<i>Strombosia scheffleri</i>	17	17	NS
<i>Bersama abyssinica</i>	17	-	NS
<i>Millettia dura</i>	17	-	NS
<i>Myrianthus holstii</i>	17	-	NS
<i>Nuxia floribunda</i>	17	-	NS

guineense, *Strombosia scheffleri* and *Newtonia buchanani*, *Tabernaemontana stapfiana*, *Macaranga neomildbraediana*, *Sapium ellipticum*, *Albizia gummifera*, *Grewia mildbraedii* and *Xymalos monospora*).

For gaps formed in 1996 (table 4), one species has a significantly lower frequency in invaded plots (*Chrysophyllum gorungosanum*) (p = 0.047). Four species are lacking in non-invaded plots. In plots invaded by the liana, 12 species are lacking.

Gaps dominated by the liana have a Simpson Index of 0.88, whereas the recorded value of 0.97 was obtained in the plots without *Sericostachys scandens*. This shows that the species diversity is higher in the gaps where *Sericostachys scandens* does not grow.

DISCUSSION AND CONCLUSION

Our assessment of the impact of invasion of *Sericostachys scandens* is based on a floristic comparison of invaded and non-invaded plots. This is a straightforward method which has very often been applied to the analysis of the impact of invasive species. However, this method assumes that, apart from the presence of the invasive species, no other factors can explain differences in floristic composition. We have no direct proof that this condition is met here and therefore, our interpretation of the results must take this limitation into account. However, we have incorporated the age of gaps in our design. This allows us to monitor the dynamics of impacts during gap closure.

When pooling all gap class ages, there are ten species which are not found in gaps invaded by *Sericostachys scandens*. These can be divided into two groups depending on the stage of vegetation (primary or secondary forest) where they are common. The first half is usually observed in primary forests (*Chrysophyllum gorungosanum*, *Newtonia buchananii*, *Symphonia globulifera*, *Syzygium rowlandii*, *Zanthoxylum gillettii*) and the second group is frequently encountered in secondary forests (*Alangium chinense*, *Cassipourea gummiflua*, *Grewia mildbreadii*, *Maerua bussei*, *Xymalos monospora*). Interestingly, in the gaps dominated by *Sericostachys scandens*, most of the remaining tree species are usually found in secondary forest. Therefore our results point out two major impacts of the liana on the dynamics of the forest, with species of primary forests being more affected by the invasive species.

There is evidence that *Sericostachys scandens* competes intensely with trees when it forms a blanket below the gap. In central Panama, Schnitzer & Carson (2010) tested a 'biotic interference' hypothesis i.e. that competition between growth forms (lianas vs. trees) constrains shade-tolerant tree recruitment, survival and diversity in gaps. They observed that removing lianas increased tree growth, recruitment and richness. In Ghana, Toledo-Aceves & Swaine (2008) tested the effect of lianas on tree regeneration in gaps in a tropical forest. Seedlings of the trees *Nauclea diderrichii* (pioneer), *Khaya anthotheca* (non-pioneer, light-demander) and *Garcinia kola* (non-pioneer shade bearer) were planted with the lianas *Acacia kamerunensis* (fast growing) and *Loeseneriella rowlandii* (slow growing) in large and small gaps. They observed that in large gaps, *Acacia* reduced significantly the biomass of *Nauclea* by 32% and *Khaya* by about 50%.

According to Parren & Bongers (2001), Bongers et al. (2002), Schnitzer & Bongers (2002), and Parren (2003), lianas are one of the main plant groups in tropical forests with a considerable negative impact on forest regeneration (Schnitzer et al. 2000). The study on Amazonian forest regeneration in Bolivia by Perez-Salicrup (2001) also indicated that the gaps without lianas have had highest regeneration capacity in contrast to the gaps with lianas and other young vegetation. In Panama, Grauel & Putz (2004) highlighted the negative impact of *Dalbergia brownei* liana on the growth of *Prioria copaifera*.

The regeneration mechanism is naturally stimulated by sunlight that reaches gaps within the forests (Rollet 1983; Brokaw 1985; Veblen 1992). In the case of KBNP, *Sericos-*

tachys scandens cover prevents the light from penetrating to the soil surface and ultimately impairs the growth of young trees.

The low relative frequencies of species found in the gaps dominated by *Sericostachys scandens* are explained by their aboveground coverage. Thus, it is possible that the rarity of species of the primary forest found in the old gaps dominated by the liana is due to their need of sufficient light to grow. According to the results of our investigation, it is clear that the expansion of *Sericostachys scandens* in KBNP forest gaps hinders species abundance and richness. Thus, it appears to inhibit forest regeneration in this area, and forest dynamics may be compromised. This study is the first to document the impacts of the liana *Sericostachys scandens* on forest regeneration in D.R.Congo. The observed impacts are sufficiently profound to raise serious concerns on the dynamics of invaded forests. Long term monitoring of vegetation in invaded plots is necessary.

ACKNOWLEDGMENTS

We thank The Belgian Development Cooperation for the financial support and Royal Belgian Institute of Natural Sciences for the scientific technical support. We thank Prof. David Mosango for the great help in polishing our English version and commenting the earlier draft. We thank the Institut Congolais pour la Conservation de la Nature which allowed us to carry out this research in the Kahuzi-Biega National Park.

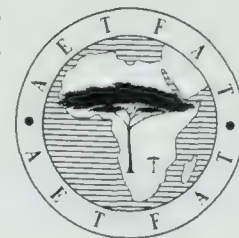
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Manuscript received 2 Aug. 2010; accepted in revised version 4 Jul. 2011.

Communicating Editor: Elmar Robbrecht.



Patterns of plant species richness of temperate and tropical grassland in South Africa

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Background and aims – The grasslands of southern Africa are threatened by habitat transformation and invasive alien species. However, the resultant plant species loss per unit area cannot be quantified, as the true richness of grassland have not been determined accurately and current estimates of richness are generally based on once-off site visits. The aim of this study was to quantify and compare the species richness of selected transformed and untransformed grasslands of tropical and temperate regions in South Africa. The study sites were located in four grassland vegetation units: KwaZulu-Natal Coastal Belt and Maputaland Woody Grassland (tropical), and Paulpietersburg Moist Grassland and Rand Highveld Grassland (temperate).

Methods – Thirty-two plots of 10 × 10 m were sampled at the four sites, namely eight in each of the vegetation units. At each site four plots were sampled in untransformed grassland and four in adjacent transformed grassland. Thorough floristic sampling of each plot was undertaken three times during the peak growing seasons.

Key results – Plant species richness was higher for untransformed grassland than transformed grassland, and is higher than what was previously estimated. Species richness is not severely affected by alien cover and richness, as species losses are made up by better adapted native and alien species entering the transformed habitat. Rare species and habitat specialists are displaced. The type of transformation has a pronounced effect on species richness.

Conclusion – Plant species richness of grassland is higher than previous estimates. Increasing alien cover and richness reduces the species richness of certain grassland growth forms and replaces species of conservation importance such as endemics.

Key words – Alpha diversity, invasive aliens, plantations, species richness, temperate grassland, tropical grassland.

INTRODUCTION

Grasslands are so called based on the structural facet of this vegetation type. Grasslands are dominated by species of the Poaceae, are mostly one-layered in structure with few trees and shrubs, and are climatically controlled (Mucina & Rutherford 2006). Grasslands occur in both temperate and tropical regions of the world. In southern Africa, Mucina & Rutherford (2006) consider grasslands to be either sub-tropical or temperate. The differentiation between these two grassland types is based on the factors responsible for the maintenance thereof. Tropical grasslands are often regarded as secondary (e.g. fire maintained) or edaphic (e.g. shallow water table) (Matthews et al. 1999). Temperate grasslands are thought to be naturally maintained by subzero temperatures and dry

winters, in combination with fire, which prevent colonisation of grasslands by the tropically-derived tree flora of southern Africa (Bredenkamp et al. 2002).

South African grasslands are characterised by plant species with special modified underground organs which enable them to escape fire (e.g. geoxyllic suffrutices; White 1977) or become dormant in winter (e.g. geophytes; Tainton & Mentis 1984) when growing conditions become unfavourable. Such adaptations are thought to be major mechanisms whereby grassland plants survive severely cold, dry winters and subsequent fires in temperate southern African grasslands (Bredenkamp et al. 2002). Grassland species, especially perennial forbs, are usually quick in responding to the effects of fire and such plants are characterised by profuse flowering and mass seed production (Retief & Van Wyk 2002).

Grasslands of southern Africa have always been considered to be diverse (Matthews et al. 1993). Before the revised account on the vegetation of southern Africa was published (Mucina & Rutherford 2006), it was difficult to make informative comparisons regarding the plant species richness of South African grasslands. The benchmark for grassland richness, according to Mucina & Rutherford (2006), is 9–39 species in 100 m² of grassland with a single structure (i.e. treeless grassland) and 19–49 species in 100 m² of multi-structural grassland (i.e. groundlayer, shrub layer and tree layer). However, a study by Siebert et al. (2002) had previously revealed that single-layered grasslands have a species richness of 25–51 species per 100 m² and multi-layered grassland 45–66 species per 100 m². These findings were probably regarded as inflated and left out of the estimation, as the study was conducted in a Centre of Endemism and could not be regarded as the norm for southern Africa for extrapolation purposes. The hypothesis, that the plant species richness of southern African grasslands is higher than was previously thought, therefore still stands. The purpose of this study was therefore to determine the species richness patterns of grasslands in South Africa and to quantify native species losses as a result of habitat transformation.

MATERIALS AND METHODS

Study area

Study sites were selected so as to represent both the tropical grasslands of the Indian Ocean Coastal Belt Biome and the temperate grasslands of the Grassland Biome (fig. 1). Vegetation units sampled from the former include the 'Maputaland Woody Grassland' (MWG) and 'Kwa-Zulu-Natal Coastal Belt' (KCB) (Mucina & Rutherford 2006). In the case of the former, the name used by Mucina & Rutherford (2006) is incorrect, and from here onward the correct name as given in Matthews et al. (1999) will be used, namely 'Maputaland Woody Grassland'. Vegetation units of the Mesic Highveld Grassland Bioregion of the Grassland Biome were sampled, namely the 'Rand Highveld Grassland' (RHG) and 'Paulpietersburg Moist Grassland' (PMG) (Mucina & Rutherford 2006). For comparative purposes, the vegetation units were chosen to represent extreme climatic conditions from hot and humid to cold and dry (table 1).

Sampling, data collection and analysis

Eight plots were sampled in each of the four study sites in different vegetation units. Care was taken to place four plots 1 km apart in grassland areas in close proximity to what is

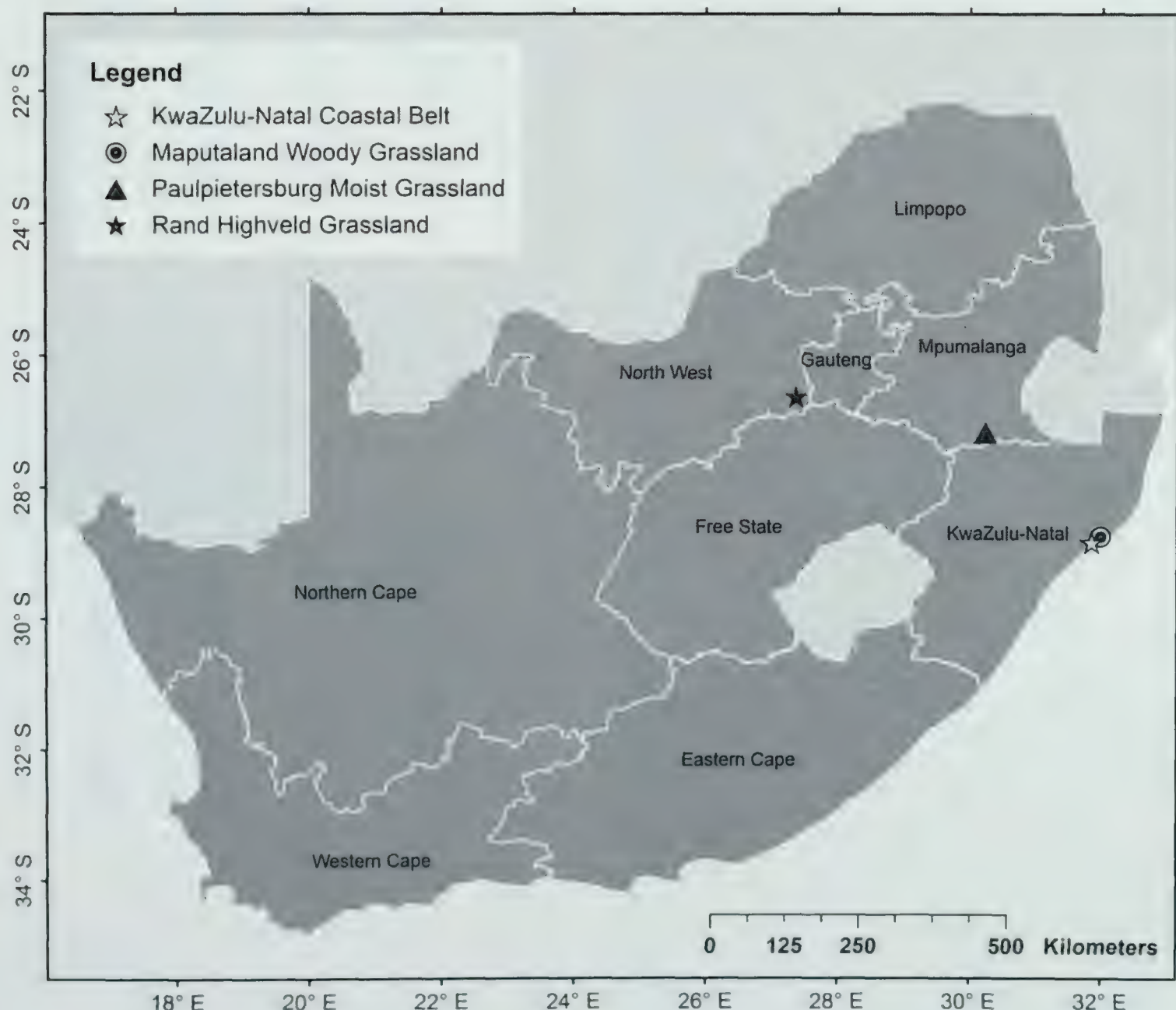


Figure 1 – Localities of the four study sites in South Africa and the associated vegetation units.

Table 1 – Climate details for the vegetation units in which the four study sites were located.

	Mean annual precipitation (mm)	Mean annual temperature (°C)	Mean frost days (< 0°C)	Mean annual soil moisture stress (%)
Maputaland Wooded Grassland	964	21.0	0	68
KwaZulu-Natal Coastal Belt	989	19.6	0	65
Paulpietersburg Moist Grassland	902	16.8	11	69
Rand Highveld Grassland	654	15.8	28	76

regarded as the most transformed areas within each of the study sites. Such transformed areas have undergone a land-use change which has changed the structure of the vegetation beyond the definition of South African grassland as described by Mucina & Rutherford (2006). A second set of four plots were then sampled within these transformed areas of each of the study sites. Each sample plot in grassland was therefore associated with a neighbouring plot in transformed grassland, not more than 150–200 m apart. In the case of MWG, transformed areas were defined as grassland invaded by alien invasive trees (e.g. *Melia azederach*) and shrubs (e.g. *Lantana camara*) for the past ± 25 years, and transformed grassland of KCB were *Eucalyptus grandis* plantations abandoned for ± 15 years. The transformed grasslands of the drier interior were defined as river banks invaded by *Acacia mearnsii* for ± 15 years in the case of PMG, and maize (*Zea mays*) fields cultivated for ± 20 years represented transformation in RHG. All plots were sampled on three occasions, namely in October, December and February, during the peak growing season. The surveys were repeated to ensure that minimal plant species were overlooked.

Plot size was fixed at 10 × 10 m (Eckhardt et al. 1996) for comparative purposes. At each sample point, the 100 m² plot was subdivided into 25 quadrants of 4 m² each for recording the species richness. Data from the 25 quadrants was then lumped to compile a complete floristic inventory for each plot. Species richness, the most direct measure of alpha diversity, was determined for each plot. However, species richness is an incomplete surrogate for alpha diversity as measures of species diversity are based on relative abundance and richness (Wilsey et al. 2005). Therefore, the number of individuals per species was counted in each quadrant (abundance) and lumped together per plot to calculate the Shannon-Wiener Diversity Index:

$$H = - \sum (p_i \ln p_i)$$

Low species abundance does not suggest low cover. As alien species invasions of native grassland takes place from the edge where the cover of such species is highest (Cilliers et al. 2008), it was important to record species cover. This was calculated per species as: $C_{sp} = \text{abundance} \times \text{mean crown diameter at widest point}$.

Species were distinguished as native or either naturalised and/or invasive aliens. Plant species names follow Germishuizen et al. (2006) and naturalised and invasive categories are according to Bromilow (2001) and Henderson (2001). Voucher specimens are housed at the University of Zululand Herbarium (ZULU), Pretoria National Herbarium (PRE), KwaZulu-Natal Herbarium (NH) and AP Goossens Herbarium (PUC).

RESULTS AND DISCUSSION

The untransformed grasslands sampled for this study, of both tropical and temperate grasslands, had a mean plant species richness of 61 ± 6 species per 100 m². This is more than the previously regarded 26 (up to 48) plant species per 100 m² based on mean data provided by O'Connor & Bredenkamp (1997), 45 (up to 51) species per 100 m² for single-layered grassland (Mucina & Rutherford 2006) and even within the range of 55 to 95 species per 1000 m² recorded by Cowling et al. (1989) for grassland. However, the above authors based their estimates on grassland richness excluding alien num-

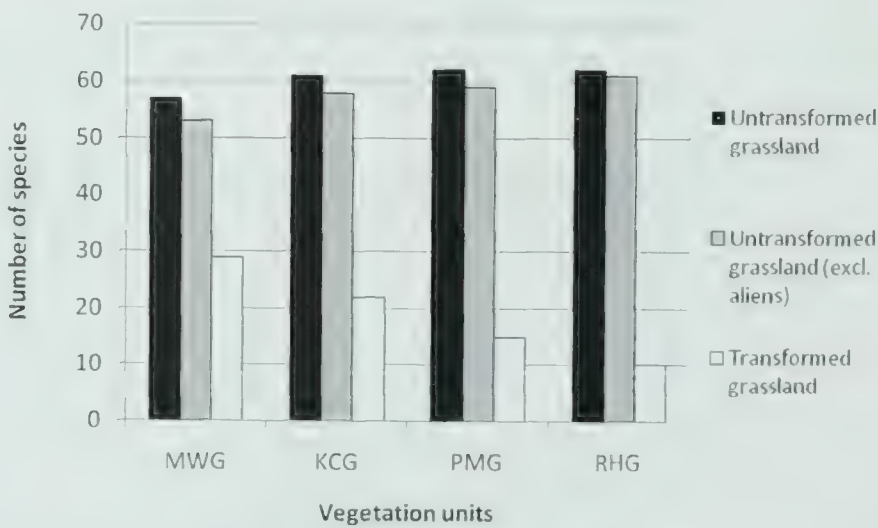


Figure 2 – Mean plant species richness per unit area (100 m²) of untransformed and transformed grassland in each of the vegetation units. Tropical grassland: MWG, Maputaland Wooded Grassland; KCG, KwaZulu-Natal Coastal Belt; Temperate grassland: PMG, Paulpietersburg Moist Grassland; RHG, Rand Highveld Grassland.

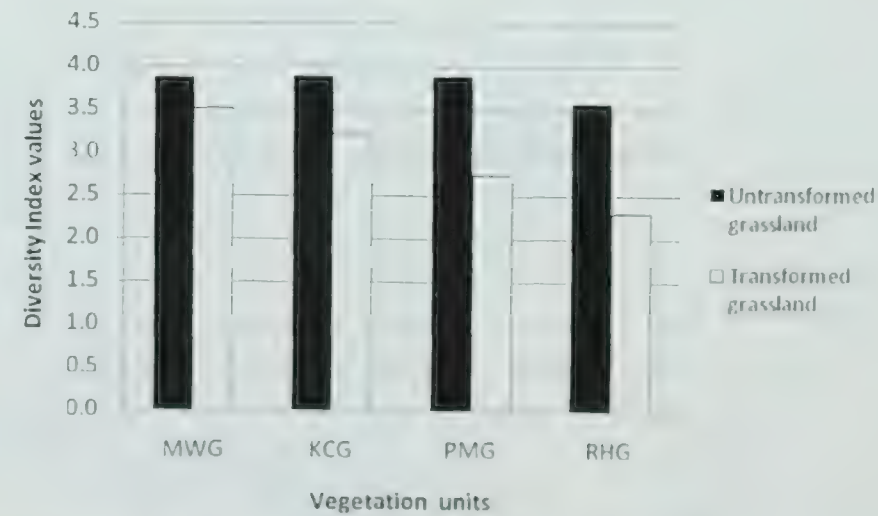


Figure 3 – Mean Shannon-Wiener Diversity Index values of untransformed and transformed grassland in each of the vegetation units. Tropical grassland: MWG, Maputaland Wooded Grassland; KCG, KwaZulu-Natal Coastal Belt; Temperate grassland: PMG, Paulpietersburg Moist Grassland; RHG, Rand Highveld Grassland.

Table 2 – Ten largest plant families of the combined study sites and the number of species per family for untransformed and transformed grassland.

Family	Number of species per family		
	Combined	Untransformed	Transformed
Asteraceae	88	69	37
Poaceae	73	56	36
Fabaceae	59	50	29
Apocynaceae	24	22	5
Cyperaceae	19	19	7
Convolvulaceae	13	9	5
Lamiaceae	11	10	4
Acanthaceae	11	10	3
Rubiaceae	10	7	4
Hyacinthaceae	9	9	2
Total	317	261	132

bers and with specific focus on temperate grasslands. When only vegetation units from the Mesic Highveld Grassland Bioregion are considered (excluding the tropical grasslands) and only native species are included in calculations, the plant species richness is 60 ± 6 species per 100 m^2 . This result is substantially more than what was previously regarded as the norm for 100 m^2 . These results also compare favourably with the findings of Siebert et al. (2002) that suggested the possibility of temperate grasslands to generally carry more than fifty species per 100 m^2 . I speculate that the low estimates of grassland plant species richness is because the phytosociological studies that generated the species data for richness calculations are based on single site visits and are ‘snapshots’ of the flora which excludes dormant or non-flowering species. Phytosociological data from South Africa generally provide biased estimates of floristic data due to once off visits to sample plots. The multiple surveys of sample plots for this study provided opportunities to record species during the peak of their specific growing seasons which allowed for a more comprehensive floristic inventory.

Transformed grasslands have lower species richness than untransformed grassland per unit area (fig. 2). The mean plant species richness for transformed grassland was 31 ± 8 with aliens included, and 19 ± 8 species per 100 m^2 without. When abundance is brought into the equation, the Shannon Wiener diversity index revealed a pattern of diversity corresponding with richness, with the index values of transformed sites being lower in all cases (fig. 3). Diversity indices also take the frequency (or abundance) of species into account, scoring lower for sites where species numbers are low and are dominated by a few species (with high abundance). Hence, when only transformed grassland is considered, then maize fields scored the lowest diversity value due to low species richness and dominance by a single species, whereas invaded grassland scored the highest. The latter usually consists of localised invasions, with patches of native species in-between, resulting in higher combined diversity. This suggests that the plot size of 100 m^2 is too large to evaluate the impact

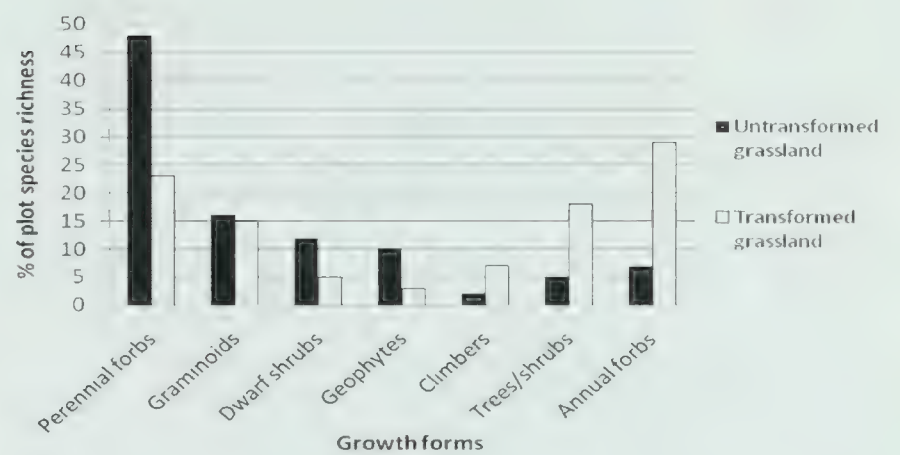


Figure 4 – Contribution that each growth form makes toward the mean species richness per plot for either untransformed or transformed grassland.

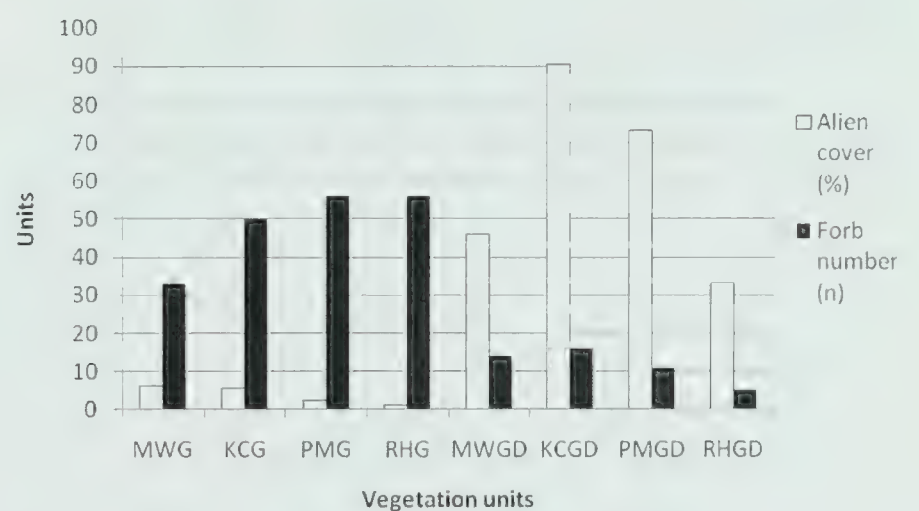


Figure 5 – Mean number of forb species and alien cover percentage per plot depicted separately for transformed and untransformed (acronyms ending with D) grassland of the different vegetation units.

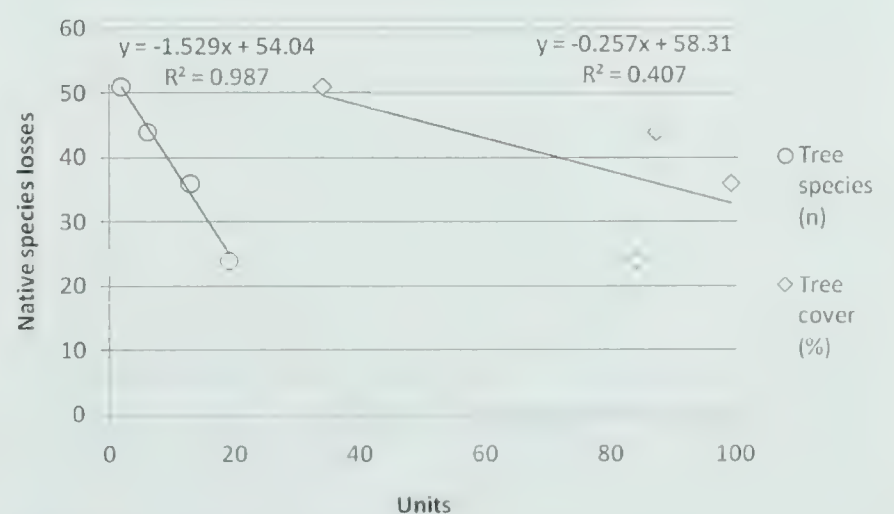


Figure 6 – Native species losses plotted against tree species richness and tree cover percentage for each of the four vegetation units. Native species losses = untransformed native species richness - transformed native species richness.

of alien invasions on native species richness in grassland as the patchiness of invasion is diluted by the numerous, interspersed non-invaded areas. Maize fields on the other hand, are exposed to added nitrogen and subsequent eutrophication, which has been shown to lead to losses in diversity and changes in plant species composition (Wedin & Tilman

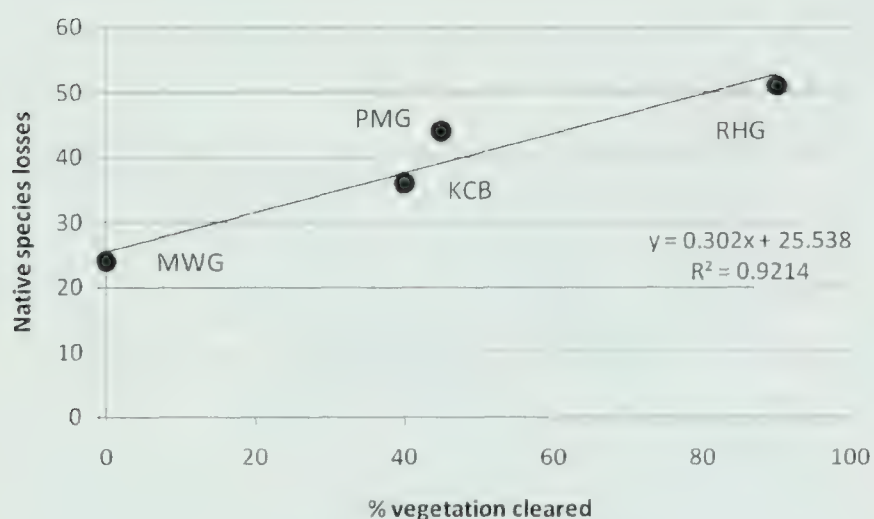


Figure 7 – Native species losses in transformed grassland plotted against a gradient of disturbance depicted here as the percentage of vegetation cleared at onset of disturbance. Onset vegetation loss was based on gross estimates obtained from the landowner.

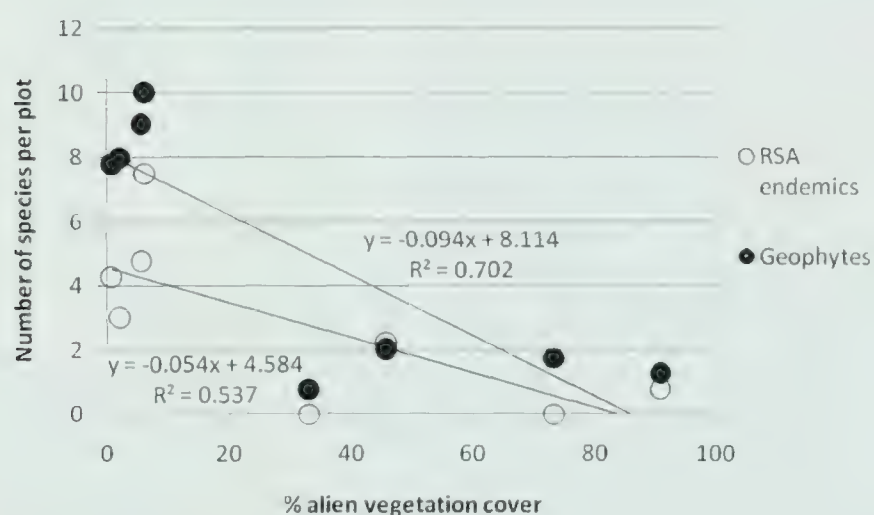


Figure 8 – Negative correlation between alien vegetation cover and the number of South African endemics and geophytes recorded from untransformed and transformed grassland in each of the vegetation units.

1996). This also makes the system vulnerable to invasions by alien species and inhibits natural succession.

Analysis of floristic data at family level suggested a loss of species from transformed grassland (table 2). This could be due to the profound effect that alien cover has on the richness of untransformed grasslands (Belcher & Scott 1989). Considering that each study site consisted of plots in untransformed and adjacent transformed grassland, comparisons could be made. Although grasslands, as the name indicates, is generally recognisable and distinguishable according to its grass assemblages (O'Connor et al. 2003, Siebert et al. 2004), the greatest variety lies with its associated forb species (Matthews et al. 1993, 1999). Forb species (excluding annual and grass species) are a good indicator of the health of the grassland ecosystem, as these species are specifically adapted to specific habitat types, and make up the bulk (> 45%) of the diversity in untransformed grasslands (fig. 4). 'Forbs' refer to perennial forbs, dwarf shrubs and geophytes. In contrast, annual forbs contribute the most to overall richness in transformed grassland (fig. 4). In the transformed grasslands sites there is the formation of new vegetation structures and the associated plant functional trait responses will be similar to what would be expected during normal grassland succession

from grassland to forest (Kahmen & Poschlod 2004). This is already evident for the transformed grassland areas. When the alien cover was between 30 and 90%, the mean 'forb' richness was 5–15 species per 100 m² (fig. 5) compared to an alien cover of below 10% in untransformed grassland that is associated with a 'forb' richness of 30–55 species per 100 m² (fig. 5).

The shading effect of trees is known to decrease forb richness in grasslands of the northern hemisphere (Pykäla et al. 2005) and is known to aid the conversion of grassland communities to woodlands (Siemann & Rogers 2003). However, these trends were not conclusive for the study sites as is evident from regressions of native species losses against number of tree species and tree cover respectively (fig. 6). In both cases native species losses decrease as the cover and richness of tree species (mostly alien) increases. Invaded grassland therefore has the least losses of native species, despite its above average tree species richness and high alien cover. Obviously there is another factor at play, and in this case it is the hidden effect of comparing different disturbances (and processes) with one another. There could be many transformation effects, but it is probably the frequency whereby vegetation is cleared (e.g. annually for maize fields), the extent of vegetation clearance (fig. 7) and time since abandonment (Zhang & Dong 2010) that have a pronounced influence on variation of species richness and diversity. Native species losses in invaded grassland are a slower process as no initial clearing of vegetation takes place. However, invasion does lead to local shading and loss of species of which proof lies in the comparison of transformed and untransformed plot richness. The rate of species loss is slow and a result of habitat fragmentation. On the long run native species will be lost from the invaded habitat as fragmentation reduces colonization rates in species rich grasslands (Joshi et al. 2006). In all the transformed grasslands similar losses of key grassland species occurred, such as geophytes and South African endemics (fig. 8), suggesting that vegetation clearing and shading effects are equally severe in reducing the richness of species of conservation priority.

CONCLUSIONS

There is a definite pattern in the richness of untransformed and transformed grassland per unit area, irrespective of whether the grasslands of two different biomes were considered. In all cases the richness of untransformed grasslands was higher than that of transformed grasslands. Species richness of untransformed grasslands was also higher than previous estimates. Future studies will have to consider recording species richness for 1 m² to make data comparable with European studies.

The term 'pattern' refers to predictable variation in species richness. In this study this variation was quantifiable and measured against different levels of transformation. In all cases the density of alien species resulted in lower diversity for transformed grasslands. Cover percentage of alien species led to changes in the growth form composition and a decrease in the forb species richness of transformed grasslands. These findings were repeated across different transformations irrespective of the grassland type.

Although the results showed that species losses were not necessarily a result of increasing tree cover or tree richness, findings did, however, lead to a proposal that the type of transformation has a more immediate effect on species losses with the frequency and extent of clearing affecting the species pool much more severely. Transformations were of such an extent, that even the plant family composition of untransformed versus transformed grassland had changed.

ACKNOWLEDGEMENTS

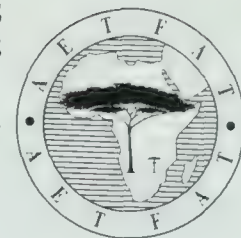
I am indebted to various South African funders, namely the National Research Foundation, South African National Biodiversity Institute and University of Zululand. Marié du Toit kindly prepared the locality map.

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Manuscript received 23 Jul. 2010; accepted in revised version 15 Apr. 2011. This paper was pre-published on 15 Nov. 2011 in issue 144(3) of *Plant Ecology and Evolution*.

Communicating Editor: Elmar Robbrecht.



Diversity and conservation value of Gabon's savanna and inselberg open vegetation: an initial gap analysis

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Background and aims – Eighty per cent of Gabon's territory is covered by forest with most species inventory work focused on these areas. However, herbaceous open vegetation types are abundant in this country and can be found in savannas on the coast, in the centre and in the south, and on inselbergs. The species diversity patterns of these habitats remain largely unexplored yet are targeted for both conservation and development. Here, we evaluate the floristic diversity of savannas in Gabon, their affinities with the inselberg open vegetation, and their contribution to the national park system in Gabon, which is currently undergoing a gap analysis. We then use a case study from the Batéké Plateaux to demonstrate species rarity in a single savanna.

Materials and methods – Species presence in the grassy formations of the savannas in Loango, Lopé, Pongara, and Plateaux Batéké national parks and in Kum inselberg is compared using ordination and clustering based on a similarity matrix (Sørensen index). For the Batéké Plateaux savannas, the species rarity and distributions are assessed using Star ratings.

Key results – The species in the open herbaceous vegetation in Gabon account for at least 11% of the total flora of the country (508 species out of 4,710). Except for the coastal savannas, all sites are highly dissimilar in floristic composition (Sørensen index 0.065–0.26) and no dominant savanna type occurs within the dataset. The inselberg site is the most dissimilar and constitutes a separate vegetation unit. Most savanna species of the Batéké Plateaux area are widely distributed, but not weedy. A few are extremely rare and are linked with moist habitats, substrate, and fire occurrence. Our results show the diversity and the conservation value of open, herbaceous habitats. Currently, the Gabonese National Park network is partly protecting the savanna and inselberg vegetation. However, several areas remain un-assessed and merit further exploration.

Keywords – Conservation, diversity, floristics, inselberg, protected area, savanna.

INTRODUCTION

The flora of Gabon is estimated to comprise as many as 7,000 species (Sosef et al. 2006) with most of the country being covered by forest (estimated at 80%). The highest species diversity and number of endemics are thought to be found in the forested montane areas (Sosef 1994) and along the coastal plane of Gabon (Ikabanga 2010, Ngagnia Ndj-abounda 2010). While several studies have focused on forest diversity patterns (Hardy & Senterre 2007, Parmentier et al. 2007), few have considered open areas such as savannas.

Collections from these areas continue to be of low density, and specialists working on the Central African flora are surprised that common herbaceous savanna species have not yet been recorded in Gabon (pers. comm.: S. Phillips, Kew Gardens, Richmond, UK and J. van der Maesen, Wageningen University, the Netherlands). Indeed, grassy formations in Central Africa are perceived to contain only widespread species, which has led botanists to devote less time to inventories of savannas, sometimes only spending a single day in the field and using the literature to supplement their collec-

tions (e.g. Cable & Cheek 1998). However, given a lack of time spent collecting in this habitat, the 'wide-spread species' assumption may not be correct. Furthermore, the existing information has only marginally been used for comparative studies exploring the diversity patterns and suggesting conservation measures. As such, it is difficult to understand the conservation value of Gabon's open, herbaceous vegetation, and whether it is sufficiently conserved in the protected area system. This is an important concept to understand as there are currently efforts both to conserve (through creating new protected areas) and to transform (through planting oil palm) savanna areas in Gabon.

Currently, Gabon's protected area system is undergoing a gap analysis to justify current areas and identify new ones that would complement Gabon's protected area network to ensure that it provides adequate coverage of the country's habitat and species diversity (e.g. Margules & Pressey 2000). These studies include work on bird, mammal, reptile, endemic plants, and a habitat analysis. This paper contributes to the open habitat analysis.

Development is also planned for some savanna areas of Gabon: in the form of oil palm plantations. Despite oil palm having been an active industry in Central Africa since the colonial period (e.g. Coquery-Vidrovitch 1987, Lynn 1989), an increase in production is foreseen in Gabon. In the coming years, some 200,000 ha of Gabon will be planted, with a focus on the southern savanna areas of Mouila, Ngounie, Nyanga and Tchibanga (Présidence de la République Gabonaise 2010). The question then is, why conserve or develop these open, herbaceous areas?

Koechlin (1962) described Gabon's savannas according to species composition and dominance of graminoid and woody species and then classified them into three categories: coastal, enclosed interior and vast interior savannas. White (1983) deemed these grasslands to be mostly 'secondary' but also containing some small, edaphic savannas. He indicated that the secondary grasslands fringing the Guineo-Congolian forest "show considerable local variation in floristic composition, but most of their constituent species are widespread and occur both north and south of the equator". His species list included tree and grass species, but provided no list of forbs. A full assessment of the floristic diversity of these savannas, including forbs, has never been conducted, though it has been proposed by others (Dauby 2007, Harris et al. in press). In recent years, several protected areas in Gabon encompassing savannas representative of the three types recognized in Koechlin's classification have been inventoried, including: Loango and Pongara National Parks on the coast; La Lopé National Park's large enclosed savanna in the interior; and the Plateaux Batéké's vast continental interior savannas.

The most similar open natural habitat to savannas in Gabon are those found on inselbergs (a German term for "islands hills"). Inselbergs are rocky outcrops standing out from encircling plains as isolated hills or groups of hills. Many inselbergs embedded in the rain forest are partially covered with open vegetation including natural grassland and herbaceous fringes (Parmentier et al. 2005). Several studies on inselberg vegetation in Gabon, Equatorial Guinea

and Cameroon have been conducted in the last decade (Reitsma et al. 1992, Ngok Banak 2005, Parmentier & Müller 2006, Parmentier et al. 2006a, 2006b).

The creation of protected areas in Gabon began during the colonial era but was formalised under the Gabonese administration starting in the early 1960s with the recognition of a series of hunting reserves (Wilks 1990). Wilks (1990) proposed new areas for protection, including the savanna areas of Ozouri (coastal lakes area) and the Batéké Plateaux around Lékoni. He also mentioned two savanna areas in south-western Gabon that were then classified as 'Réserves Naturelles' but that have since been declassified, viz. Kouri and Ndende. Prior to the establishment of thirteen new national parks (NPs) in Gabon in 2002, gap analyses indicated that the protected area system was not representative of the country's biodiversity and habitats; the forest-savanna mosaic was considered to be under-represented and of ecological importance for conservation (Doumenge et al. 2001, 2003b). Other sites have since been proposed, including two for the forest-savanna mosaic at Okandja (northern Batéké Plateaux) and Fouari (southern Tchibanga forest-savanna mosaic) (Doumenge et al. 2003a). The current protected area network of Gabon includes thirteen national parks and several protected areas, of which eight that contain areas of savanna: Batéké Plateaux NP, La Lopé NP, Pongara NP, Loango NP, Mayumba NP, Moukalaba-Doudou NP, Arboretum de Raponda Walker, and the Wonga Wongue Presidential Hunting Reserve. Only one contains inselbergs (Minkébé NP).

Botanists continue to place national floras within a global context by citing numbers of species and rates of endemism (e.g. Davis et al. 2009). Such comparisons help the scientific and conservation communities to identify diverse areas and gaps in their knowledge, thereby orienting future collecting and conservation efforts (Sosef et al. 2006). However, these accounts usually do not take into consideration the global distribution of taxa. The use of Star ratings makes it possible to evaluate taxa (and the communities in which they occur) based on their distribution range, and has been used in Cameroon (Cable & Cheek 1998, Tchouto et al. 2006), Gabon (Sosef et al. 2004), Ghana (Hawthorne & Abu Juam 1995) and Central America (Gordon et al. 2004). Nearly every previously published approach using this system has, however, focused on forest communities; this paper presents its first proper publication for herbaceous vegetation.

Both savannas and inselbergs contain herbaceous vegetation, however, the similarity between the inselberg and the savanna floras has not been formally tested and their relative contribution to species and habitat conservation in Gabon has not been analysed. We present here the first floristic comparison of the open herbaceous vegetation of Gabon, asking five questions: (1) what is the overall contribution of these species to Gabon's floristic diversity, (2) how does species composition differ amongst geographic areas, (3) are inselbergs grassland savanna islands? (4), do some savannas contain globally rare species? and (5) what is the contribution of these floras to Gabon's national park system?

Table 1 – Summary of study site characteristics.

Site	GPS coordinates	Rainfall (mm per year)	Altitude (m)	Species in each grassy, open formation	Total number of collections (specimens from all habitats)	References
Batéké Plateaux NP	2°07'S 14°03'E	2,000–2,890	400–700	175	~ 1,725	Bout 2006, Walters 2010
Kum inselberg	1°50'N 11°38'E	1,843	740	68	347	Parmentier et al. 2006a, 2006b, Parmentier & Müller 2006
Loango NP	1°50'S 9°20'E	2,000–2,363	0–100	136	~ 1,954	Harris et al. in press
Lopé NP	00°12'S 11°36'E	1,500	100–700	217	> 2,500	Korte 2007, Leal 2004, McPherson et al. (unpubl. res., Missouri Botanical Garden, St. Louis, USA)
Pongara NP	00°16'N 9°19'E	2,000–3,100	0–40	85	586	Dauby et al. 2008

STUDY SITES

The savannas of four National Parks and the grassy formation in one inselberg in Gabon were chosen for this analysis: savannas of Loango and Pongara on the coast, La Lopé and the Kum inselberg in the centre and north, and the Ba-

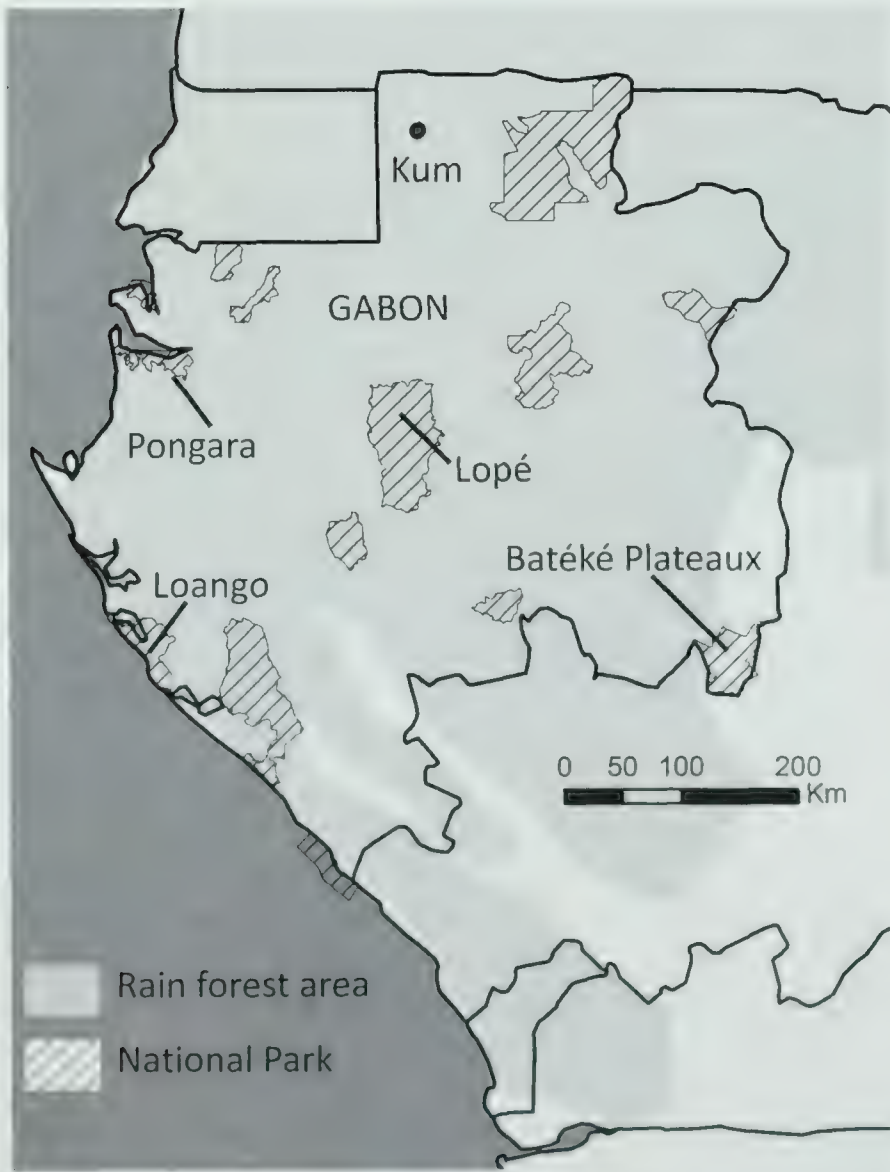


Figure 1 – Location of the 5 study sites in Gabon (West Central Africa): four savanna areas and one inselberg (Koum).

téké Plateaux in the south-east (fig. 1). Gabon is located on the Equator and has one long dry season (June–September) during which anthropogenic and sometimes natural fire is prevalent in the savannas; there is a long rainy season (October–May), punctuated by one to two small dry seasons (December–March). In these mesic savannas, there is a mixture of trees (reproducing via post-fire re-sprouting rather than from seed), herbs, and C₄ grasses (eg. Ratnam et al. 2011). The study sites receive 1,500–3,100 mm of rainfall per year and are located between elevations of 0–740 m (table 1). On the inselberg, due to shallow soils, environmental conditions vary from very dry, with high temperatures and high levels of evapotranspiration, to very humid where water flows and accumulate (Parmentier & Müller 2006). Given that there are no existing estimates of the size of the study areas and that there is no accurate vegetation map reliable for all study areas in order to use a GIS to calculate these areas, we include the ‘total number of collections’ as a measure of collection effort of each of the study areas and so an estimation of size and completeness of the floristic lists compared.

Despite the debate over the use of the word ‘savanna’ to describe African herbaceous formations which seeks to categorise them according to the percentage of woody cover (see Lowry et al. 1997, White 1983), these formations in Gabon vary in cover and height of vegetation within short distances making the utilisation of this classification difficult without good woody cover estimations or precise collection notes using the same system (see Walters 2010). For those following White’s classification, the herbaceous formations described in this paper correspond to shrubland, grassland, wooded grassland, transition woodland, herbaceous freshwater swamp and aquatic vegetation types (as described in Lowry et al. 1997, White 1983). Here we use the word savanna for all of these categories where (1) graminoid species are continuous, interrupted by trees and shrubs, (2) fires occur, and (3) growth is closely associated with alternating wet and dry seasons (Bourliere & Hadley 1983). We do not consider roadside vegetation or saline herbaceous formations in this work. All of the savannas under study here have been

Table 2 – Star ratings detailed by range of distribution (Hawthorne 1996).

Star	Estimated range in no. degree squares in Africa	Notes
Black	1.6 ± 0.5	Rare globally and rare in Gabon. Urgent conservation attention required.
Gold	7.8 ± 3.8	Rather rare globally and locally. Conservation attention required.
Blue	24.5 ± 12.6	Widespread globally but rare in Gabon; or widespread in Gabon but rare globally. Some conservation attention from Gabon required.
Green	69.2 ± 49.8	No conservation concern.

formed under previous climatic conditions which favoured the expansion of savannas (Delègue et al. 2001, Maley 2001). Many of these savannas are part of the country's cultural heritage, containing sites of archaeological and anthropological value (Oslisy 2001, Dupré & Pinçon 1997, Walters 2010). As a prime example, La Lopé NP is classified as a mixed biological and cultural UNESCO World Heritage site.

METHODS

Fieldwork and dataset composition

The analyses in this paper are the result of data obtained from fieldwork by GW in the Batéké Plateaux conducted between 2000 and 2009, by GW in Loango National Park in 2005 and by IP in the Kum Inselberg area in 1999 and 2002. For other sites, we used data from the checklists of Pongara (Dauby et al. 2008) and La Lopé (McPherson & White 1995). Specimen identifications were made at BR, K, LBV, MO, and WAG.

The taxa from the open habitats of each site were extracted from the species lists, and names were standardized according to the Gabon Checklist (Sosef et al. 2006). The data from the different sites were pooled into a global list of 508 taxa that was used to calculate the proportion of the species in the Gabon Checklist that are present in the savanna and in the inselberg sites included in our study.

Floristic similarity of all sites

A cluster analysis was conducted on the species lists of each of the five sites (Group average, Sørensen similarity index) using *Primer6*© (Clarke et al. 2006). Species similarity between site pairs, i and j , was estimated using the Sørensen similarity index C_{ij} (Sørensen 1948) because it is regarded as one of the most effective for comparing presence/absence data between samples (Southwood & Henderson 2000). The index was calculated as follows:

$$C = \frac{2a}{2a + b + c}$$

where a is the total number of species present in both samples, b the number of species present only in sample i and c the number of species present only in sample j . Clustering was made using the group average method (Clarke 1993). An ordination analysis of the five sites was then completed using Non-metric Multi-Dimensional Scaling (NMDS) using *Primer6*© based on the Sørensen similarity matrix. Options used for NMDS were: Kruskal stress formula = 1; minimum stress = 0.01; number of restarts = 100. The hierarchical classification obtained by Clustering was represented on the or-

dination diagram using the 10 and 20% similarity cut. The geographical distance between pairs of sites was calculated. Correlation was then used to infer the relationship between the Sørensen similarity index and inter-site distance.

Evaluation of species distribution and rarity in the Batéké Plateaux

The distribution for each species of the Batéké Plateaux list was obtained from botanical references such as national or regional floras (e.g. the *Flore du Gabon*) and on occasion from the original species description. Only species that were fully identified were used thus removing fourteen species from the list. Using the Star rating system and the same degree-square assignments proposed in Hawthorne & Abu-Juam (1995), these distributions were then categorised. The four main Stars in the Star rating are summarized in table 2.

RESULTS

Floristic similarity of all sites

The species of the five study sites represent 10.8% of the currently known flora of Gabon (508 of 4,710 species), with savanna species alone representing 9.6% (453 species) of the flora. The floristic composition is highly different among all sites, with Sørensen similarity indices ranging between 0.065 and 0.26. Only one species (*Sauvagesia erecta* L.) is shared among the five sites, and just eighteen species have been recorded at four sites. The inselberg site has the most distinct species composition and the two coastal savannas are the most similar to one another, although even these still exhibit a high level of dissimilarity (fig. 2).

There is only a weak correlation of floristic similarity with inter-site distance when all sites are considered ($r^2 = 0.08$). However, when Kum inselberg is excluded (leaving only savanna sites), the correlation value slightly increases ($r^2 = 0.28$).

Evaluation of species distribution and rarity in the Batéké Plateaux

A total of 183 herbaceous and woody species have been recorded from the savannas of the Batéké Plateaux. Forty-seven of these species (26%) are rare in Gabon, known only from Haut Ogooué Province, although all of them have distributions extending beyond the borders of the country. When considering the global rarity of these species, 89% correspond to the Green Star category, i.e. they are widely distributed; 6% were classified as blue species, 1% were as-

Table 3 – Batéké Plateaux globally rare species.

Family	Species	Star	Factors apparently limiting distribution
Apocynaceae	<i>Asclepias occidentalis</i> Goyder	Gold	Post-fire emergence; Kalahari Sands Specialist (Goyder 2009)
Cyperaceae	<i>Scleria baroni-clarkei</i> De Wild	Gold	Unknown (Piérart 1953)
Eriocaulaceae	<i>Syngonanthus ngoweensis</i> Lecomte	Black	Moist Savanna (Kimpouni 1992)
Eriocaulaceae	<i>Syngonanthus schlechteri</i> Ruhl.	Gold	Moist Savanna (Kimpouni 1992)
Fabaceae	<i>Eriosema batekense</i> van der Maesen & G.M.Walters	Black	Kalahari Sands Specialist (van der Maesen & Walters 2011)
Verbenaceae	New species	Gold	Kalahari Sands Specialist (P. Bamps, Meise, Belgium, pers. comm.)

signed a Gold star, and another 1% a Black Star. The distribution of these rare Black and Gold species appears to be limited by edaphic conditions (related to the presence of the Kalahari Sands substrate), periodic inundation, or burning (table 3). All star ratings and the data matrix can be found in the online supplement (electronic appendix).

DISCUSSION

This analysis suggests that despite the fact that open herbaceous vegetation is present on inselbergs (grasslands and herbaceous fringes, Parmentier & Müller 2006), the flora of these inselberg micro-habitats is very different from the savanna flora. Open inselbergs and savanna floras clearly represent separate vegetation units.

Inselberg are not savanna islands in the rain forest

Very low floristic similarity between savannas and the open herbaceous inselberg vegetation of the Kum inselberg reinforces the results of earlier studies in which inselberg vegetation in Gabon, Equatorial Guinea and Cameroon was described in detail (Parmentier & Müller 2006, Parmentier et al. 2006b). The flora of the inselberg grasslands and herba-

ceous fringes is a different mix of species from the rain forest, ruderal and secondary forest elements, strictly saxicolous taxa and species restricted to the inselberg habitat (e.g. *Epistemma rupestre* H.Huber, *Euphorbia letestui* J.Raynal, *Plectranthus inselbergi* B.J.Pollard & A.J.Paton, *Tricarpelema africanum* Faden). Inselbergs surrounded by rain forest show insular properties, with species similarity between sites declining with distance (Parmentier et al. 2005). At a local scale, species composition is best explained by the edaphic conditions along the forest-inselberg ecotone, corresponding to an array of ecological niches (Parmentier 2003), but at the regional scale, theses ecological niches are occupied by different species. These sub-regional species pools probably result from the history of past vegetation changes due to climatic fluctuations (Parmentier & Hardy 2009). The inclusion of floristic data from other inselberg sites in Gabon (of which there are many) would therefore certainly contribute additional species to the overall list of taxa from open grassy vegetation in Gabon.

Floristic similarity among savannas

This analysis shows that, as indicated by White (1983), the savanna floras of Guineo-Congolia are floristically varied, even when the forb component is considered. The dissimilarity in composition of the sites studied here is probably related to a variety of factors including substrate age and type, savanna age, phytogeography, and inter-site distance. Since our sample size is not sufficient to elucidate cause, we will just note some observations for further investigation.

Both edaphic and climatic factors have shaped savanna floras in Gabon (Droissart 2009, Delègue et al. 2001, Maley 2001, Delire et al. 2008). Limited seed dispersal may also explain species dissimilarity between sites, as it did for inselbergs. While the correlation for similarity of species among the four savanna sites was linked to inter-site distance, it was weak; this relationship might become strengthened with the addition of more study sites.

Given the floristic dissimilarity, it should also be noted that the woody dominants and edge colonisers in each savanna are also different thus requiring locally adapted management approaches (Mouandza-Membo & Walters 2007, Jeffery et al. 2011). Recent studies suggest that the savannas in each of these areas are being encroached by forest (Delègue

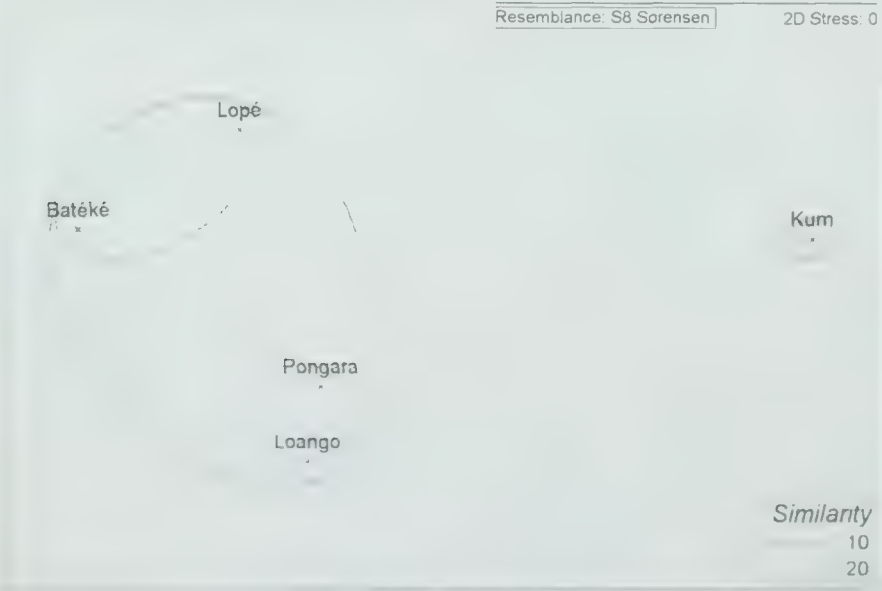


Figure 2 – Ordination of the five sites using Non-metric Multi-Dimensional Scaling obtained from a Sorensen similarity matrix. Lines delineate groups obtained by clustering and applying a cut of 10 and 20% of similarity.

et al. 2001, Leal et al. 2007, Nana 2005), a common occurrence also in Cameroon (Mitchard et al. 2009), and the Republic of Congo (Dowsett & Dowsett-Lemaire 1991, Favier et al. 2004, Schwartz et al. 1996). This phenomenon is particularly relevant to protected areas established to preserve savanna, as in the case of La Lopé (Palla 2011, Walters 2010).

Evaluation of species distribution and rarity in the Batéké Plateaux

Vegetation work in the Batéké Plateaux savannas began in earnest in the 1970s (e.g. Makany 1972, 1976). However these studies were conducted prior to the discovery or description of most of the area's endemic species, many descriptions of which included historic and new collections (eg. Goyder 2009, van der Maesen & Walters 2011, Kimpouni 1992). This study takes into account these recent discoveries. The results presented here indicate that savanna vegetation contains six globally rare species which are classified as Black or Gold Stars. Moreover, the six globally rare species in the Batéké Plateaux are those restricted to either the Kalahari sands substrate or moist savannas, or among those subjected to fire; these species can be added to the list of those that are endemic to the southern Kalahari sands (e.g. Walters et al. 2006).

The rarity of some species in the Batéké Plateaux savannas suggests that more collection effort should be made in these habitats. This result is similar to observations for the coastal, wet savannas in Equatorial Guinea (Phillips 2000), for both the Niari and Plateaux Batéké savannas in Gabon (Descoings 1975), and for the Loango savannas (Harris et al. in press). The discovery of these species comes through collection and identification efforts in savanna areas by specialists in herbaceous floras; indeed, recently more than thirty new records for the flora of Gabon have come from savannas, including the discovery of rare species (Harris et al. in press, Walters et al. 2011).

Star Ratings were not available for all species in all sites in this study meaning that the associated Genetic Heat Index could not be calculated. Future work in using the Star Rating system to generate Genetic Heat Indices will be helpful in assessing the relative value of areas for conservation (e.g. Tchouto et al 2006). It is suggested that future work focus on assigning Star rating for the species in these and other areas.

Current protection of savanna and inselberg sites

Representation of a nation's biological diversity is one reason for which protected areas are created (Margules & Pressey 2000). Many assessments of Gabon's protected area system have focused only on evaluating the species diversity of forests; however, savannas and inselbergs also deserve conservation attention. Recent work on assessing the floristic similarity of both forest and savanna taxa from four national parks (Minkébé, Monts de Cristal, Loango, and Batéké Plateaux) in Gabon has found that the floras of these parks are extremely different (Wieringa & Sosef 2011). Our study produced similar results for the open, herbaceous vegetation in the five sites in this study; indeed, with the present level of

analysis, it is impossible to identify any dominant savanna types in Gabon, if they exist. These studies suggest that the savanna and forest floras currently protected are different and contribute to representing Gabon's flora; as such, their protection is justified. However sufficient data to analyse all savannas and inselbergs in Gabon are lacking as a result of low collection density in other sites (Sosef 2010). While the savannas studied here have been well prospected, three key savanna areas in Gabon need further collections in order to be assessed: Tchibanga, Franceville-Boumango, and Wonga Wongue. This includes some of those savannas currently proposed for oil palm plantations.

Most of the country's inselbergs are found in the continental forest that extends east of the Monts de Cristal towards Minkébé NP. Only a group of inselbergs in Minkébé NP are currently protected, while the site examined in this study remains unprotected. With the exception of a single study (Ngok Banak 2005), almost nothing has been published about the inselberg flora of the Medouneu area, which harbours hundreds of inselbergs, as indicated by an aerial survey conducted in 2001. The conservation value of the inselbergs in this area was recognized by USAID's Central African Regional Program for the Environment when defining the Monte Alén and Monts de Cristal inselbergs Landscape. However, most of these sites are located in logging concessions and lack any conservation status. We therefore suggest that inselbergs should be a priority in management plans submitted by forest companies to the Gabonese government.

The open, herbaceous areas of Gabon are variously being conserved or developed; however, our results indicate diversity and potential rarity of some species in these areas. This underscores the importance of study before action. However, until better specimen coverage is made available through additional inventory work across all sites, the data for analysing aspects of the flora, including the geographic distribution of herbaceous and woody floristic diversity, will remain limited.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consist of a list of star ratings and a species matrix used for ordination analysis (pdf format).

ACKNOWLEDGMENTS

This work was supported by grants to the first author from the Rufford Foundation, The University College London Graduate School, the Parkes Foundation, and Synthesys-EU for visits to BR and WAG. I. Parmentier (post-doctoral researcher) is financed by the Belgian Fund for Scientific Research (FRS-FNRS). The curators of BR, K, LBV, MO, and WAG are acknowledged for access to their collections. Identifications of some Batéké Plateaux species were provided by D. Harris, O. Lachenaud, P. De Block, S. Phillips, M. Sosef, D. Goyder, L.J.G. van der Maesen, S. Dessein, and P. Bamps. The directors of the *Herbier National du Gabon*, the *Institut de Pharmacopée et Médecines Traditionnelles*,

the *Projet Protection des Gorilles-Gabon* are thanked for institutional support. Species lists for Lopé NP were provided by G. McPherson and for Loango by D. Harris. Discussions with W. Hawthorne were particularly helpful in addressing the use of Star ratings, with J. Wieringa for understanding patterns of floristic similarity in Gabon, and with Michelle Lee on conservation planning. Thanks to L.J.G. van der Maesen, P.P. Lowry, and W. Hawthorne for their review of earlier versions of this manuscript.

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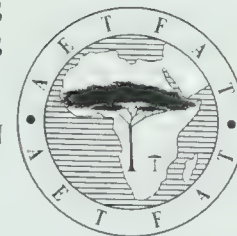
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Manuscript received 31 Oct. 2010; accepted in revised version 25 Nov. 2011. This paper was pre-published on 12 Mar. 2012 in issue 145(1) of *Plant Ecology and Evolution*.

Communicating Editor: Laurent Gautier.



Coastal dry forests in northern Mozambique

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Background and aims – The Coastal Forests of Eastern Africa, stretching along the Indian Ocean coastline from Somalia to Mozambique, are considered by Conservation International to be a global biodiversity hotspot – an area of high diversity and endemism under increasing threat. Although the largest remaining extent of these forests is reported to be found in Mozambique, very little is known on their extent, condition and composition here. In addition, the term ‘coastal forest’ has been used in different ways by different authors. This paper defines and characterises coastal dry forests found in northern Mozambique and assesses their present extent, botanical composition, conservation importance and the threats to these forests.

Methods – The study area of 18,150 km² lies in Cabo Delgado Province in north-east Mozambique, adjacent to Tanzania. Its limits are determined primarily by geological substrate and landform. Four smaller study sites were chosen covering a range of landforms. Manual interpretation of satellite imagery dating from 1999–2002 was used to calculate possible previous and present extent of ‘dense vegetation’. Extensive field collecting was used in determining botanical composition and distribution patterns. IUCN Red List assessments were carried out on selected species using distributional criteria.

Results – Dry forests similar to those in southern Tanzania are found widely scattered across coastal Cabo Delgado, sitting in a matrix of miombo woodland and other vegetation types. However, forest cover is not as extensive as was believed. We calculate that the original extent of ‘dense vegetation cover’, which includes coastal dry forest, was 6087 km². Owing to clearance over the last 150 years this is now only 1182 km², of which perhaps only 400 km² is moderately-intact dry forest.

In this southern part of their range such forests are essentially dry, not moist and mesic, and dominated by a high proportion of deciduous or sclerophyllous evergreen trees. The plant species composition differs significantly from that of the surrounding woodlands. There is a marked change in species composition between forest patches along the coast, and they contain numerous species with restricted global distribution. Since 2003, 68 species new to Mozambique have been recorded from Cabo Delgado in addition to 36 possible new species. Many new records are of species previously only known from south-eastern Tanzania. Previously recorded patterns of restricted distribution and high species turnover between forest patches in Kenya and Tanzania are confirmed. Seven coastal forest species were assessed as Endangered.

Regional context and conservation – Coastal dry forests are discussed in relation to the more widespread ‘sand forests’ of the continental interior of south-central Africa, and shown to have similarities in ecology, species composition, soils and ecology. Very little of the present extent of coastal forests in Mozambique lies within protected areas. The threats to their continued existence in the face of exploitation for timber, agriculture and oil exploration are outlined.

Key words – Mozambique, coastal forest, endemics, hotspot, conservation.

INTRODUCTION

The Coastal Forests of Eastern Africa are considered by Conservation International (CI), an international conservation organisation, to be a global biodiversity hotspot – an area of high species diversity and endemism that is under increasing threat (Myers et al. 1999, Burgess et al. 2004b). The same area along the eastern African coastline has also been recognised by the World Wide Fund for Nature (WWF) as a globally important ecoregion – the Eastern Africa Coastal Forest Ecoregion (Burgess et al. 2004a) – with a specific programme directed towards its conservation (WWF-EARPO 2006). This hotspot or ecoregion extends from southern Somalia through Kenya and Tanzania to southern Mozambique (fig. 1), although most of our knowledge on the area comes from studies in Kenya and Tanzania (e.g. Moomaw 1960, Greenway 1973, Brenan 1978, Robertson & Luke 1993, Hawthorne 1993, Vollesen 1994, Burgess & Clarke 2000, Burgess et al. 2004a).

It has often been assumed that the major extent of remaining intact vegetation in this hotspot lay in northern Mozambique in the provinces of Cabo Delgado and Nampula (Burgess et al. 2000, Burgess et al. 2004a, WWF-EARPO 2006), but to date there has been little direct evidence of this in terms of mapped forest extent. Historical plant collections from the 1940s to mid-1960s suggested that some restricted-range species, otherwise only known from coastal southern Tanzania, were also found here (Brenan 1978, Clarke et al. 2000: 137) along with some Mozambique endemics, but the extent of forest remaining and the significant presence of range-restricted or endemic species was speculative.

Following the instability resulting from the independence and civil wars, development is now occurring at a rapid rate in the country, including exploration for onshore oil and gas, and this is likely to accelerate the loss of what remains of these coastal forests. The investigation of coastal northern Mozambique is an obvious priority for botanists and conservationists.

Coastal Mozambique falls within what White (1983) terms the Zanzibar–Inhambane regional mosaic, a phytochorion stretching along the East African coast from Somalia down to South Africa. This area has a distinctive flora, different from that found further inland in the Zambezian regional centre of endemism. Unfortunately, White did not map any of the coastal dry forest patches within this rather broad regional mosaic, and his descriptions of dry forest vegetation is skewed towards that found in Kenya. Within the mosaic he describes ten vegetation types of which four (Zanzibar–Inhambane undifferentiated forest, Zanzibar–Inhambane transition woodland, Zanzibar–Inhambane woodland and scrub woodland and Zanzibar–Inhambane secondary grassland and wooded grassland) seem to occur in north-east Mozambique. Much of the Cabo Delgado study area falls within what White calls Zanzibar–Inhambane woodland and scrub woodland. Surprisingly, he does not explicitly recognise dry coastal forest as a separate type in Mozambique, unlike Wild & Barbosa (1967) on which much of White's work for the country was based.

More recently, on the basis of species richness and composition, Clarke (1998) has split White's Zanzibar–Inham-



Figure 1 – Area with coastal forests in Eastern Africa (adapted from Burgess et al. 2004b).

bane regional mosaic into two separate phytochoria – the Swahilian regional centre of endemism in the north and the Swahilian/Maputaland regional transition zone in the south.

The only vegetation maps available for this part of northern Mozambique are those by Pedro & Barbosa (1955) and the Flora Zambesiaca vegetation map (Wild & Barbosa 1967), which was partly based on the former. Both maps show that Cabo Delgado has a somewhat different vegetation from other parts of Mozambique, and that most of it is covered in a type of miombo woodland. However, these maps show areas of Dry Deciduous Lowland Forest on the Mueda plateau, a vegetation type that appears to have largely disappeared, and, of particular interest to us, Dry Deciduous Thicket with *Guibourtia schliebenii* (Harms) J.Léonard, the type that formed part of the main focus of the present study.

In recent years there has been renewed interest in coastal Mozambique. In 2003, Quentin Luke, who had previously studied the moister coastal forests of Kenya and northern Tanzania, visited Cabo Delgado on behalf of WWF and CI and collected a number of new plant records (Luke 2006), followed by John and Sandie Burrows in 2005–2008 in the course of writing a tree field guide for Mozambique. Results from these collections are incorporated here. In 2008, the French NGO Pro-Natura International, together with the Muséum National d'Histoire Naturelle in Paris, obtained funding to carry out preliminary biological surveys of plants and various vertebrate and invertebrate groups in this hotspot in Cabo Delgado Province, resulting in two major expeditions in 2008 and 2009. Other institutional partners in the study were the Instituto de Investigação Agrária de Moçambique, the herbarium of the Royal Botanic Gardens, Kew and the Buffelskloof Herbarium in Lydenburg, South Africa.

This paper outlines initial findings on the extent and botanical composition of forests in Cabo Delgado Province arising from these recent expeditions and studies, and discusses their links to similar dry forests elsewhere in Eastern and Southern Africa.

WHAT ARE COASTAL FORESTS?

The term ‘coastal forest’ has been used widely in recent years (e.g. Hawthorne 1993, Robertson & Luke 1993, Myers et al. 1999, Burgess et al. 2004a, Burgess & Clarke 2000, Clarke 2000a, WWF-EARPO 2006) but there has been inconsistency in definition. In some cases, most of the dense vegetation formations found in the coastal area (e.g. within 100–150 km of the coast) or within White’s (1983) Zanzibar–Inhambane phytchorion are included, whilst others (e.g. WWF-EARPO 2006) have included various forest or woodland formations (except mangroves) up to 300 km inland, possibly as they were lowland vegetation types or contained some species with a typically East African coastal distribution. But unless such coastal species are dominant they can not realistically be termed coastal forests.

Clarke (2000a) formally defines East African Coastal Forests as forests (i.e. a continuous stand of trees with crowns overlapping or interdigitating, usually comprising several layers and/or interlaced with lianas, often with a sparse or absent ground layer) dominated by Swahilian endemic or near-endemic tree species, and describes six different types. The term is used collectively to encompass both typical Eastern African coastal dry forests as well as variant and transitional formations where they share features with forests of other phytchoria. On the other hand, Hawthorne (1993) adopts a more geological and geomorphological definition, defining ‘coastal’ as lying on sedimentary (or volcanic) sediments of the coastal plains and plateaux, excluding any vegetation formations on Basement Complex substrates.

However, in practice areas termed ‘coastal forest’ shown on some recent maps have covered a wide range of vegetation from dense woodland through dry forest to true moist forest. More importantly, in some cases there appears to be no common or linking feature between these ‘forest patches’ in terms of species composition or ecology, which has led to confusion in determining the distribution of coastal dry forests in Mozambique, their biodiversity attributes, ecology, possible origins and conservation significance. The assumed commonality in terms of the origin and conservation importance of this group of vegetation types has masked our understanding of them, and perhaps inhibited selection of important or representative areas for conservation.

In this study we have attempted to define ‘coastal forest’ in a more restricted way, at least as regards those in northern Mozambique. It is hoped this definition and understanding will apply equally well to forests in Tanzania south of the Rufiji River.

We define coastal dry forest here as essentially dry forest or thicket formations that are found within 50–100 km of the coast. These are generally vegetation formations with a closed or almost-closed canopy (80% cover or more when undisturbed) with a high proportion of deciduous woody species that lose most of their leaves during the long dry season. The definition does not include moist forest, i.e. forest dominated by species with non-drought adapted leaves, nor does it include vegetation that is dominated or characterised by what are primarily woodland species (such as *Brachystegia* or *Julbernardia*). Moist forests of the continental interior may contain some tree species that are found in coastal forests, but,

unless such species are dominant, this does not mean they are coastal forests. These moist forests, miombo and similar woodlands and mangroves are excluded, as is vegetation associated with watercourses such as rivers. Coastal dry forests are characterised as much by their species composition as by their physical structure (which can of course be modified by land uses such as logging or cultivation). Under our definition the main characteristics of coastal dry forests are:

- Dry, deciduous and semi-deciduous forest (80% canopy cover or more), becoming thicket-like with disturbance. The main species are not moisture-demanding or even mesic. They occur in areas subject to a lengthy dry season (in excess of 6 months), with the majority of tree species responding by losing leaves.
- Contain a significant number of sclerophyllous evergreen tree and shrub species in the understorey.
- Have a species composition significantly different from that of the surrounding woodland (mostly miombo). The overlap in species composition between the two types is often less than 30%.
- Have a very patchy distribution, and are often apparently restricted to particular soils, such as unconsolidated sands, and geomorphological positions, such as in the upper part of the catena.
- Show a marked change in species composition between patches with very few species found regularly or widely. There are a high number of species of restricted distribution, often from particular families and genera (e.g. Annonaceae, Leguminosae: Caesalpinioideae, Rubiaceae).

Typical sclerophyllous species commonly found in coastal forests across Cabo Delgado include *Manilkara sansibarensis* (Engl.) Dubard, *Warneckea sansibarica* (Taub.) Jacq.-Fél. and *Baphia macrocalyx* Harms, while *Pteleopsis myrtifolia* (M.A.Lawson) Engl. & Diels and *M. sansibarensis* are among the very few that are found in most forest patches.

STUDY AREA

The study area runs the length of Cabo Delgado Province in north-eastern Mozambique from the Rovuma river, the border with Tanzania, south to Pemba, with an extent of 18,150 km² (fig. 2). Forming a long triangle, about 280 km at its longest and 100 km at its widest, between Mueda and Mocímbo do Rovuma in the west, Quionga and the Rovuma estuary in the northeast, and Pemba in the south, its limits are based on geology and landform, encompassing only Cretaceous and more recent deposits. Full details are given in Timberlake et al. (2010).

Four smaller study sites were chosen (fig. 2) on the basis of their apparent good condition and size, uniqueness and accessibility, and as they were different from each other in terms of landscape and substrate.

- a) Pundandar–Nangade in Palma and Nangade Districts, west of the Nhica area along the W-E higher ground associated with the Rio Rovuma, including a hunting concession (approx. 750 km²).
- b) Palma–Nhica do Rovuma area in Palma District, along the W-E higher ground associated with the lower reaches of the Rio Rovuma and along the main road south from

Palma (approx. 1400 km²).

- c) Quiterajo in Macomia District, situated on the coast 45 km south of Mocímboa da Praia, just south of the Rio Messalo (approx. 750 km²).
- d) Lupangua in Quissanga District inside the Quirimbas National Park, 15 km south of Quissanga and opposite Ilha Mefunvo (approx. 25 km²).

Our principal focus was on coastal dry forest formations, so associated vegetation types such as *Brachystegia*-dominated miombo and similar woodlands, pan grassland and riverine formations, were only looked at in order to obtain a broader context.

Geomorphology, geology and soils

The area comprises a gently tilting interior plateau, rising from about 100 m above sea-level along the Palma–Mocímboa road to over 600 m in the west along the Mueda escarpment. However, most of our study sites lie between 80 and 180 m, although patches of dry forest were found down to an altitude of 40 m. To the east of the Palma–Mocímboa road the land drops down to a narrow coastal plain. Much of the interior plateau acts as a ‘sponge’ with pans and edaphic grasslands resulting from seasonally-poor drainage. There are numerous

drainage lines flowing to the south east or, in the northernmost section, to the north east, and some are quite deeply incised closer to the coast. On the northern margin, the Rio Rovuma has cut through these plateau sediments to create a wide valley (c. 10 km wide), forming the border with Tanzania. Similar land forms are found in south-east Tanzania.

North-eastern Cabo Delgado is seen to have a different geological origin from much of the rest of Mozambique (national geological map, ING 1987), comprising younger formations dating from the Lower Cretaceous period up to the Neogene lying adjacent to the much older continental block of Precambrian granites and other rocks. There is also a narrow coastal strip comprising uplifted recent Quaternary deposits. As strata in these apparently marine deposits are relatively level, the landform is primarily determined by differential resistance to erosion by the different strata and retreating scarp erosion, resulting in numerous flat-topped plateaux.

Nearly all the coastal dry forest patches seen were located on iron-rich sandstone and conglomerates of the Mikindani Formation (mid-Neogene, $\pm 15\text{--}10$ mya), while associated miombo and similar woodlands were found on more recent Quaternary formations (Pleistocene, $\pm 1.6\text{--}0.01$ mya). This is clearly seen in the Quiterajo area with its forest-capped plateau, but is less obvious along the Rovuma rim (Nhica do Rovuma to Nangade).

It would appear that the extent of soils derived from the Mikindani Formation, comprising coarse, unstructured, well-drained sands, red-brown in colour, and possibly quite acidic, are a major determinant of the distribution of coastal forests here. However, this link has not yet been tested and causation is not fully established.

Climate

Summary monthly data have been taken from Kassam et al. (1981), which covers various nearby localities. Rainfall is around 1000 mm/year falling in a single rainy season, while potential evapo-transpiration significantly exceeds rainfall for the period May to November–December, giving a growing season of around 4–5 months. There is a long hot dry season before a single clearly-defined rainy season from December to April, while atmospheric humidity during November and early December is high.

Although there is a coastal influence and some effects from the Indian Ocean monsoon, the climate of the study area generally follows that more typical of the continental interior. This part of northern Mozambique lies partly in the rain-shadow of Madagascar (Clarke 2000b), so has a somewhat lower rainfall than areas of the country further south or central Tanzania.

SURVEY RESULTS

Past and present extent of forest

Estimates of the remaining extent of coastal dry forest and similar formations in the study area were made using photographic copies of 1999–2002 false-colour Landsat ETM imagery at 1 : 250,000 scale. An approximation was also made of the possible original extent of dense vegetation cover some

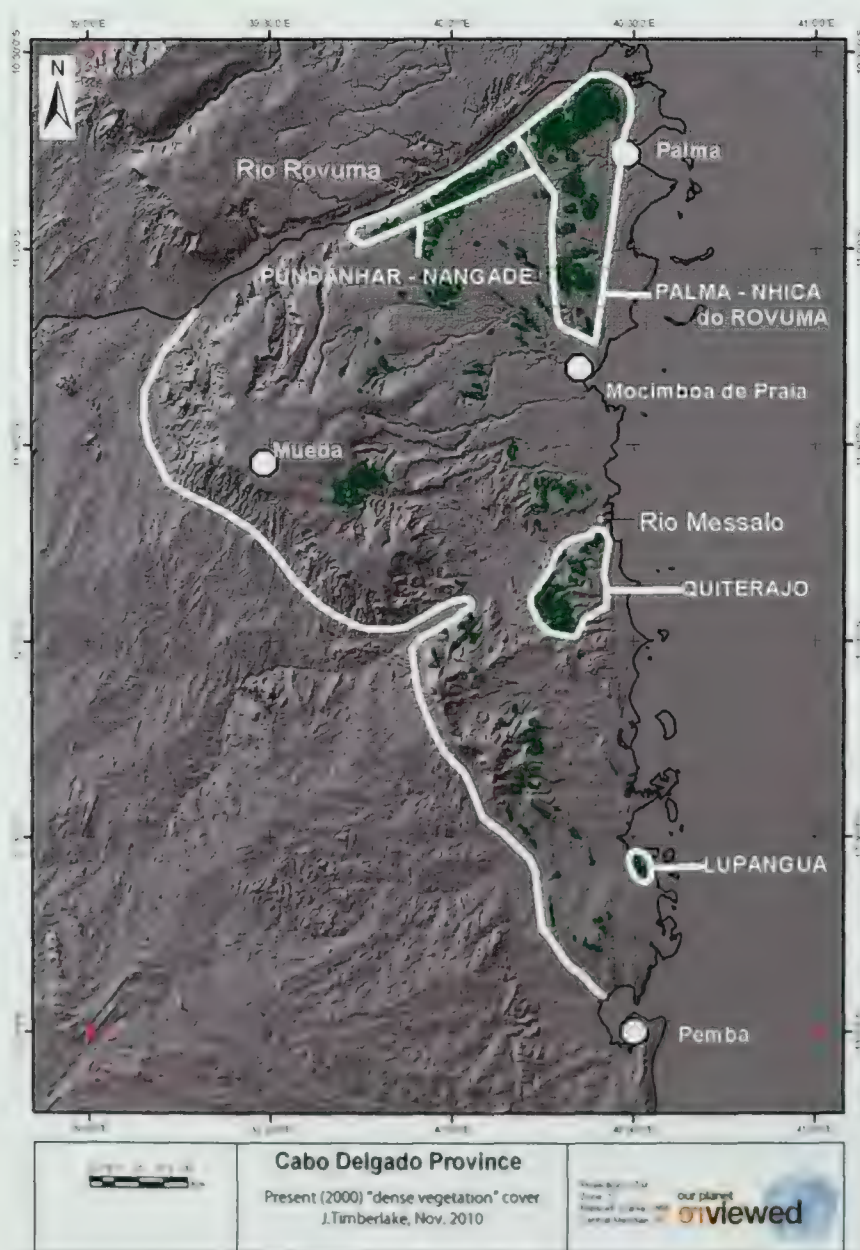


Figure 2 – Cabo Delgado study area showing the four detailed study sites (white lines), and present extent of ‘dense vegetation’ cover (green blocks).

Table 1 – Original and remaining extent of dense woodland and dry forest vegetation types, based on interpretation of 2002 Landsat imagery.

area	original extent (km ²)	present extent (km ²)		loss of dense veg. cover (%)
		dense veg. cover	dry forest	
NW, Mueda plateau & E slopes	2332	89	30	96.2
NE, Nangade–Pundanmar–Nhica–Quionga–Palma–Mocímboa	2173	769	260	64.6
EC, Rio Messalo–Quiterajo	576	166	55	71.2
S, Chai–Mucojo–Pemba, S of Rio Messalo	1006	158	53	84.3
total	6087	1182	398	80.6

100–150 years ago, before significant changes in land use occurred. Delineation was by manual interpretation using a transparent mylar sheet overlay; a dot planimeter was used to determine area. Results are presented by geographical block.

Original extent – The possible original extent of dry forest was determined using a combination of (a) suitable up-land landform, (b) underlying geology, and (c) reflectance (smooth, reddish texture on false-colour imagery). A reduced image at 1: 800,000 scale was used to obtain a better synoptic view. Based on field observations of current species composition and distribution, as dry forest patches appear to be restricted to certain soils and landscape units, it is believed that only 10% of the area delineated as ‘dense vegetation cover’ would have been dry forest, with the majority being miombo or similar woodland types. However, these figures may be significantly in error.

The suggested original extent of ‘dense vegetation cover’ was 6080 km² (table 1), and within that the extent of dry forest is estimated at around 615 km², or 3% of the entire study area. Even with a higher proportion of dry forest vs. woodland, the original extent is unlikely to have been more than 1000 km². Although the assumptions are not substantiated, given the lack of historical data this is probably the best figure that can be obtained. The main densely vegetated areas were thought to be in the north along the Rovuma margin and along the eastern slopes of the Mueda plateau, but there were also significant blocks around the lower reaches of the Rio Messalo and in the Macomia area.

Present extent – A more detailed assessment using 1: 250,000 scale images was made of the present extent of dense vegetation cover. Various key assumptions were made, including (a) that relatively smooth-textured non-mottled reddish areas on false-colour imagery indicate well vegetated sandy soils from the Mikindani Formation, most of which lie up on the plateau, while blue areas indicate woodland or grassland; (b) that deeper red-hued, ± homogeneous blocks are likely to be dry forest or dense woodland; (c) mottled areas include significant cultivation and were excluded; (d) around a third (rounded figures) of suitable substrate is likely to support dry forest patches rather than dense woodland, transitional areas or areas with just a sprinkling of dry forest species; and (e) rugged terrain along the Rovuma valley rim was included as field experience showed these areas support some good dry forest patches.

Based on these assumptions, the total extent of ‘dense vegetative cover’ was calculated to be 1182 km² in 2002, with

398 km² of this being dry forest (table 1), or 2% of the total study area. The overall loss of dense vegetation cover from the entire study area over the last 100–150 years appears to be around 80%, with losses ranging from 96% on the Mueda plateau to around 65% in the Nhica area.

The main dry forest areas are now found in the north-east part of the study area associated with the southern margin of the Rovuma valley from Pundanmar to Nhica do Rovuma, and in the Quionga area associated with the Rio Luvumba/Macanga that flow into the Rovuma estuary (fig. 2). There are also sizeable areas along the Palma–Mocímboa da Praia road. Other significant areas of dry forest include Nahavara forest near Quiterajo (31 km²) and others south of this, and the patch at Lupangua (20 km²) in the Quirimbas National Park.

It is clear that large parts of the area have been cleared for agriculture over the last 100 years, yet our field work suggests significant additional expanses have been cleared close to population centres and main roads since 2002. It is also thought that forest quality on the ground is often low owing to previous logging, old clearance for fields (5–50 years ago), and frequent fire, none of which are readily detectable on the imagery. Hence the figure of almost 400 km² of remaining dry forest extent given here is likely to be an overestimate from a conservation viewpoint.

Botanical composition

The main focus of the botanical study was on plant collection, particularly from the dry forest patches. More open vegetation types, such as around pans, on the coastal margins and in the Rovuma valley, were not well-collected. The expeditions took place just before the rains, so grasses and herbs are poorly represented. Representative sets are held at RBG Kew (K), IIAM in Maputo (LMA), and at the Muséum National d’Histoire Naturelle, Paris (P), with any additional duplicates in Maputo (LMU), Nairobi (EA) and Buffelskloof (BRNH). Earlier identifications were done by Quentin Luke (EA) and John Burrows (BRNH), with all others and confirmation done at Kew, primarily by David Goyder, Frances Crawford and Iain Darbyshire.

Over 3000 numbered collections were made during the various earlier trips and two expeditions in 2008 and 2009. A total of 738 plant taxa were recorded from 105 families, of which 36 taxa are either entirely new to science or were known previously from material too fragmentary to describe formally (table 2; see Burrows 2009, Burrows & Burrows 2010). The largest family recorded was Rubiaceae with 83

Table 2 – New and undescribed species recorded from Cabo Delgado study area, 2003–2009.

Monocotyledons
Asparagaceae
<i>Asparagus</i> ?sp. nov.
Araceae
<i>Stylochaeton</i> sp., uncertain status
Dicotyledons
Annonaceae
<i>Xylopia</i> sp. nov.
<i>Xylopia</i> sp. A of FTEA
Asteraceae
<i>Vernonia</i> ?sp. nov. aff. <i>inhacensis</i> G.V.Pope
<i>Vernonia</i> ?sp. nov. 2
Celastraceae
<i>Pleurostyliia</i> ?sp. nov. aff. <i>serrulata</i> Loes.
Convolvulaceae
<i>Ipomoea</i> ?sp. nov.
Euphorbiaceae
<i>Euphorbia</i> ?sp. nov. aff. <i>ambroseae</i> L.C.Leach
Flacourtiaceae
<i>Casearia</i> ?sp. nov.
Lamiaceae
<i>Vitex</i> ?sp. nov. aff. <i>buchananii</i>
<i>Vitex</i> cf. <i>mossambicensis</i> Gürke
Leguminosae: Mimosoideae
<i>Acacia latispina</i> J.M.& S.M.Burrows
Leguminosae: Papilionoideae
<i>Baphia</i> ?sp. nov.
<i>Erythrina</i> ?sp. nov.
Melastomataceae
<i>Warneckea</i> sp. nov.
Meliaceae
<i>Trichilia</i> ?sp. nov.
Ochnaceae
<i>Ochna</i> ?sp. nov.
Rubiaceae
? <i>Chassalia</i> cf. <i>umbraticola</i> Vatke
<i>Didymosalpinx callianthus</i> J.E.& S.M.Burrows
<i>Oxyanthus</i> sp. A of FZ
<i>Oxyanthus biflorus</i> J.E.& S.M.Burrows
<i>Polysphaeria</i> ?sp. nov.
<i>Psilanthus</i> sp. nov., cf. sp. A of FTEA
<i>Pyrostria</i> sp. B of FZ
<i>Pyrostria</i> sp. D of FTEA
<i>Pyrostria</i> ?sp. nov. = Luke 9724
<i>Rytigynia</i> cf. <i>umbellulata</i> (Hiern) Robyns
= de Koning et al. 9759 of FZ
<i>Tarenna</i> sp. 53 of Degreeef 2006
<i>Tricalysia</i> sp. A of FZ
<i>Tricalysia</i> sp. B of FZ
Rutaceae
<i>Vepris</i> sp. nov.
<i>Zanthoxylum lepreurii</i> Guill.& Perr., subsp. nov.?
Sapindaceae
<i>Deinbollia</i> ?sp. nov.
Sterculiaceae
<i>Cola</i> sp. nov. 1 aff. <i>clavata</i> Mast.
<i>Cola</i> ?sp. nov. 2 aff. <i>clavata</i> Mast.

taxa, followed by Leguminosae: Papilionoideae with 43 (table 3). The family with the largest number of new species was Rubiaceae (thirteen), followed by Annonaceae, Asteraceae, Lamiaceae, Papilionoideae, Rutaceae and Sterculiaceae with two each. A full list of species identified is given in Annex 2 of Timberlake et al. (2010). Excluding new species, 68 new records are reported for Mozambique (table 4) from the study area and immediate surrounds. We believe that this is an exceptionally high number of new records to discover anywhere in southern and eastern Africa, and indicates not just the marked lack of previous collecting, but also the richness of the area and the high number of range-restricted species.

Distribution patterns

One of the study’s objectives was to see if the patterns of local endemism recorded from the Tanzania coast, especially in the Lindi region (Bidgood & Vollesen 1992, Vollesen 1994, Clarke 1998, 2001), were also seen in coastal northern Mozambique. This would require the mapping of distributions of a large number of species using records both from this study and from herbaria elsewhere, and has not yet been done. Instead, some preliminary observations are given on broad species distribution patterns for seven selected species and on differences between vegetation types.

All available records for these seven species, known to be restricted to coastal areas and showing differing distribution patterns, were collated and mapped (fig. 3). Two species are endemic to coastal northern Mozambique [*Micklethwaitia carvalhoi* (Harms) G.P.Lewis & Schrire and *Thespesia mos-*

Table 3 – Number of taxa from the main plant families found in the Cabo Delgado study.

family	no. taxa	no. new species	no. new Moz records
Araceae	12	1	4
Orchidaceae	11	-	5
Acanthaceae	18	-	2
Annonaceae	23	2	5
Apocynaceae	28	-	2
Asteraceae	11	2	1
Capparaceae	19	-	2
Celastraceae	14	1	1
Combretaceae	17	-	-
Ebenaceae	12	-	3
Euphorbiaceae	41	1	3
Lamiaceae	28	2	3
Leg.: Caesalpinioideae	24	-	2
Leg.: Mimosoideae	29	1	1
Leg.: Papilionoideae	43	2	3
Rubiaceae	83	13	8
Rutaceae	9	2	2
Sapindaceae	12	1	1
Sterculiaceae	11	2	-
Tiliaceae	12	-	1
Vitaceae	6	-	2

Table 4 – New records for Mozambique from Cabo Delgado study area, 2003–2009.

monocotyledons	dicotyledons
Amaryllidaceae	Ebenaceae
<i>Crinum aurantiacum</i> Lehmillier	<i>Diospyros magogoana</i> F.White
Anthericaceae	<i>Diospyros shimbaensis</i> F.White
<i>Chlorophytum amplexicaule</i> Baker	Euphorbiaceae
Araceae	<i>Croton polytrichus</i> Pax subsp. <i>polytrichus</i>
<i>Amorphophallus maximus</i> (Engl.) N.E.Br. subsp. <i>fischeri</i>	<i>Drypetes sclerophylla</i> Mildbr.
(Engl.) Govaerts & Frodin	<i>Omphalea mansfieldiana</i> Mildbr.
<i>Anchomanes abbreviatus</i> Engl.	Lamiaceae
<i>Culcasia orientalis</i> Mayo	<i>Orthosiphon scedastophyllus</i> A.J.Paton
<i>Stylochaeton euryphyllus</i> Mildbr.	<i>Premna gracillima</i> Verdc.
Areceaceae	<i>Premna hans-joachimii</i> Verdc.
<i>Hyphaene petersiana</i> Mart.	Leguminosae: Caesalpinioideae
Dracaenaceae	<i>Scorodophloeus fischeri</i> (Taub.) J.Léonard
<i>Sansevieria</i> cf. <i>metallica</i> Gérôme & Labroy	<i>Senna auriculata</i> (L.) Roxb.
Orchidaceae	Leguminosae: Mimosoideae
<i>Eulophia acutilabra</i> Summerh.	<i>Newtonia paucijuga</i> (Harms) Brenan
<i>Eulophia guineensis</i> Lindl.	Leguminosae: Papilionoideae
<i>Microcoelia megalorrhiza</i> (Rchb.f.) Summerh.	<i>Dalbergia lactea</i> Vatke
<i>Microcoelia physophora</i> (Rchb.f.) Summerh.	<i>Erythrina haerdii</i> Verdc.
<i>Nervilia bicarinata</i> (Blume) Schltr.	<i>Erythrina saclexii</i> Hua
dicotyledons	Loganiaceae
Acanthaceae	<i>Strychnos xylophylla</i> Gilg
<i>Lepidagathis plantaginea</i> Mildbr.	Myrtaceae
<i>Whitfieldia orientalis</i> Vollesen	<i>Eugenia capensis</i> (Eckl.& Zeyh.) Sond. subsp. <i>multiflora</i> Verdc.
Anacardiaceae	Ochnaceae
<i>Lannea schweinfurthii</i> (Engl.) Engl. var. <i>acutifolia</i>	<i>Ochna ovata</i> F.Hoffm.
(Engl.) Kokwaro	Passifloraceae
Annonaceae	<i>Adenia kirkii</i> (Mast.) Engl.
<i>Artabotrys modestus</i> Diels subsp. <i>macranthus</i> Verdc.	Rubiaceae
<i>Lettowianthus stellatus</i> Diels	<i>Coffea schliebenii</i> Bridson (Coffea sp. D of FTEA)
<i>Monanthes taxia falknerae</i> Verdc.	<i>Gardenia transvenulosa</i> Verdc.
<i>Monanthes taxia trichantha</i> (Diels) Verdc.	<i>Kraussia kirkii</i> (Hook.f.) Bullock
<i>Monodora minor</i> Engl.& Diels	<i>Leptactina papyrophloea</i> Verdc.
Apocynaceae	<i>Pavetta lindina</i> Bremek.
<i>Baissea myrtifolia</i> (Benth.) Pichon	<i>Rhodopentas parvifolia</i> (Hiern) Kårehed & B.Bremer
<i>Cryptolepis hypoglaucula</i> K.Schum.	<i>Rothmannia macrosiphon</i> (Engl.) Bridson
Asteraceae	<i>Vangueria</i> cf. <i>randii</i> S.Moore subsp. <i>vollesenii</i> Verdc.
<i>Vernonia zanzibarensis</i> Less.	Rutaceae
Balanitaceae	<i>Vepris sansibarensis</i> (Engl.) Mziray
<i>Balanites maughamii</i> Sprague subsp. <i>acuta</i> Sands	<i>Zanthoxylum lindense</i> (Engl.) Kokwaro
Burseraceae	Sapindaceae
<i>Commiphora fulvotomentosa</i> Engl.	<i>Haplocoelum inoploeum</i> Radlk.
<i>Commiphora pteleifolia</i> Engl.	Thymelaeaceae
Capparaceae	<i>Synaptolepis kirkii</i> Oliv. sensu stricto
<i>Maerua bussei</i> (Gilg & Gilg-Ben.) Wilczek	Tiliaceae
<i>Ritchiea capparoides</i> (Andr.) Britton var. <i>capparoides</i>	<i>Grewia stuhlmannii</i> K.Schum.
Celastraceae	Violaceae
<i>Elaeodendron buechananii</i> (Loes.) Loes.	<i>Rinorea welwitschii</i> (Oliv.) Kuntze subsp. <i>tanzanica</i> Grey-Wilson
Connaraceae	Viscaceae
<i>Vismianthus punctatus</i> Mildbr.	<i>Viscum gracile</i> Polhill & Wiens
Cucurbitaceae	Vitaceae
<i>Peponium leucanthum</i> (Gilg) Cogn.	<i>Cissus phymatocarpa</i> Masinde & L.E.Newton
Ebenaceae	<i>Cissus sylvicola</i> Masinde & L.E.Newton
<i>Diospyros kabuyeana</i> F.White	



Figure 3 – Distribution records of selected coastal species. A, *Guibourtia schliebenii*; B, *Hexalobus mossambicensis*; C, *Micklethwaitia carvalhoi*; D, *Monodora minor*; E, *Scorodophloeus fischeri*; F, *Thespesia mossambicensis*; G, *Vismianthus punctatus*. Black line = extent of occurrence (EOO); red squares = area of occupancy (AOO) using 4 km² grid; blue polygon = extent of subpopulations using Rapoport's mean propinquity technique.

Table 5 – Global IUCN Red Data status for seven selected Eastern African dry forest species and 2010 assessments from the East African Plant Red List Authority (EAPRLA).

family/species	No. records	EOO (km ²)	AOO (4 km ² cell)	status	EAPRLA assessment
Annonaceae					
<i>Hexalobus mossambicensis</i> N.Robson	11	45,043	28	EN	-
<i>Monodora minor</i> Engl. & Diels	23	54,062	68	EN	NT
Connaraceae					
<i>Vismianthus punctatus</i> Mildbr.	11	22,864	40	EN	VU B1ab(iii)+2ab(iii)
Leguminosae: Caesalpinioideae					
<i>Guibourtia schliebenii</i> (Harms) J.Léonard	18	164,778	64	EN	VU B2ab(ii,iii,iv,v)
<i>Micklethwaitia carvalhoi</i> (Harms) G.P.Lewis & Schrire	8	9,502	28	EN	-
<i>Scorodophloeus fischeri</i> (Taub.) J.Léonard	72	137,578	212	EN	LC
Malvaceae					
<i>Thespesia mossambicensis</i> (Exell & Hilc.) Fryxell	5	16,416	20	EN	-

sambicensis (Exell & Hilc.) Fryxell], one shows a Cabo Delgado–Lindi distribution (*Vismianthus punctatus* Mildbr.), and three show a somewhat broader Tanzania–Mozambique coastal distribution [*Monodora minor* Engl. & Diels, *Guibourtia schliebenii* and *Scorodophloeus fischeri* (Taub.) J.Léonard], although *Guibourtia* is also found inland on the Eastern Arc mountains and *Scorodophloeus* is also found in coastal Kenya.

During the identification process it was noted that twelve taxa were endemic to coastal northern Mozambique (area Moz N: of Flora Zambesiaca) plus around nineteen of the new species. There are 53 taxa known primarily from northern Mozambique and adjacent areas of south-east Tanzania (area T8 of Flora of Tropical East Africa), showing the strong links between them. Most of these appear to be local endemics. A further 46 taxa appear to be at the southern end of their East African (Swahilian) distribution in Cabo Delgado.

It is also apparent that species in miombo and similar woodland types, fallows, grassland and wetlands, are far more widespread than those from dry forests. Many of them are found across the Miombo Ecoregion of south central Africa (Timberlake & Chidumayo 2001) or even more widely, e.g. *Azelia quanzensis* Welw., *Brachystegia spiciformis* Benth., *Parinari curatellifolia* Benth., *Pseudolachnostylis maprouneifolia* Pax and *Uapaca nitida* Müll.Arg., in marked contrast to the local distribution of so many dry forest species. An interesting exception is *Berlinia orientalis* Brenan that commonly occurs in fallows and miombo woodland (and sometimes in dry forest), but which is known only from a limited area of Cabo Delgado across to south-east Tanzania (Luke 2004).

Future work will probably confirm these distribution patterns and show the very marked East African coastal element in the overall distribution of the dry forests of the study area, with particularly strong links to that found with the Lindi–Mtwara region of south-east Tanzania, while also showing that woodland and grassland flora species have a much wider distribution.

Red Data assessments

Preliminary conservation assessments to determine IUCN Red Data List categories were carried out on the seven woody species used to map distribution patterns. All were chosen primarily for their known restricted coastal distribution patterns or ecological importance and because there were adequate data points.

By using the Kew GIS Unit's extension tool (www.kew.org/gis/projects/cats/catsdoc.pdf), rapid conservation assessments based on IUCN categories and criteria were produced (IUCN 2008). Data points were derived from collections made during this study and from historic specimens held at Kew, those available from the African Plants Initiative (<http://plants.jstor.org>) and from Missouri Botanic Garden's Tropicos database (<http://www.tropicos.org>), which includes specimens from the East African Herbarium (EA). The assessments calculate the Extent of Occurrence (EOO), Area of Occurrence (AOO), number of sub-populations and number of locations (table 5). The cell size used for AOO was 4 km² (2 × 2 km), recommended by IUCN (2008) for restricted distribution species.

From the individual species assessments, distribution maps were compiled (fig. 3) and the species' IUCN status (IUCN 2001) determined (table 5). By using the default 4 km² cell size all species were assessed as being Endangered (EN). If a larger cell sizes were used (e.g. 35–85 km sides), the threat status decreased in most cases to Least Concern. Of the seven species, the most narrowly distributed was the Mozambique endemic *Thespesia mosambicensis*, occurring in only twenty cells, while the other Mozambique endemics *Hexalobus mossambicensis* and *Micklethwaitia carvalhoi* were recorded from just 28 cells. *Scorodophloeus fischeri*, found from northern Mozambique to southern Kenya, was found in 212 cells. As the process is automated, this can lead to some odd maps, such as in fig. 3F. Here two obviously separate populations are artificially linked by the EOO, which is more an indication of the spread of risk. In this case the restricted AOO should be regarded as the more definitive indication of distribution and risk.

Conservation assessments are already available on the IUCN Red List website (<http://www.iucnredlist.org>) for three of these species – *Guibourtia schliebenii* (VU B1+2b), *Hexalobus mossambicensis* (DD) and *Monodora minor* (Near Threatened) – the first two dating from 1998 before much information was available for the Mozambique populations. Recently, four of the seven species above were assessed by the East African Plant Red List Authority (EAPRDA, Q. Luke, pers. comm.) with results shown in table 5. In three cases the assessments were lower, probably as more local information was available on their status in Tanzania and Kenya. Of particular note is *Scorodophloeus*, which the EAPRDA assessed as Least Concern rather than Endangered.

Although the preliminary assessments are based solely on recorded past and present distributions derived from herbarium specimens, we know the habitat is under marked threat, hence the Endangered status may be appropriate for some species. It is likely that a number of other dry forest species, once assessed, will have a similar threat status. In contrast, the great majority of species associated with woodland across the study area are known to have a much wider sub-continental distribution and will likely be assessed as Least Concern.

CONTEXT AND CONSERVATION

Regional context

Across south-central Africa numerous, generally small (less than 20 km²) patches of dry forest can be found within the matrix of miombo or similar Caesalpinoid-dominant woodland types (Timberlake & Chidumayo 2001, Frost et al. 2002). Examples are the extensive *Cryptosepalum exfoliatum* De Wild. forests of north-west Zambia (Fanshawe 1973, Burgess et al. 2004a, type 32); the Itigi thickets in central Tanzania dominated by *Baphia burttii* Baker f., *B. massaiensis* Taub., *Combretum celastroides* M.A.Lawson and *Bussea massaiensis* (Taub.) Harms. (Burt 1942, Burgess et al. 2004a, type 48); similar forests around Lake Mweru Wan-tipa in north-east Zambia; forest patches dominated by *Xylocarpus torreana* Brenan in the middle Zambezi valley and northern Zimbabwe (Timberlake et al. 1993, type C2); and patches characterized by *Guibourtia conjugata* (Bolle) J.Léonard on Cretaceous sands in south-eastern Zimbabwe and the northern Kruger National Park in South Africa. Sometimes termed ‘sand forests’ these vegetation types are primarily found on unconsolidated medium to coarse-textured sandy soils (often acidic) in the higher part of the catena.

Such dry forests show much similarity to many of the coastal forest patches seen in Cabo Delgado, particularly as regards the substrate, geomorphological position and in the families and even genera of characteristic plant species. As with coastal forests, there is a characteristic change in species composition across an area, and always a marked difference in species composition compared to that of the surrounding woodlands. In addition, many canopy species of dry forests of the continental interior are also early-deciduous with scattered sclerophyllous evergreen species in the understorey. With disturbance dry forest tends towards thicket, as can be clearly seen with the ‘jesse bush’ of the mid-Zambezi valley and in the Itigi thickets.

This raises an interesting question of whether all these dry forests – coastal and those on the old African plateau of the continental interior – are remnants of an earlier drier period, or whether it is a case of convergent evolution of vegetation type. However, coastal dry forests do show much higher levels of endemism and contain more species of restricted coastal distribution compared to those of the interior. For the coastal forests it is not clear if the species are relictual or, alternatively, what the driver might have been for their evolution given the relatively recent age of these patches in the landscape. The soils on which they are found are generally not old and infertile, as is the case with other areas of high endemism such as the Chimanimani mountains, Mt. Mulanje or the sandstones of the Cape mountains.

Conservation

The coastal strip of this part of Cabo Delgado has been settled for hundreds of years. Slave trading was significant during the 19th century and there was much trade at that time in ivory, gum copal (from *Hymenaea verrucosa* Gaertn.) and ‘wild rubber’ (*Landolphia* spp.). During the 20th century, in particular after the Second World War, there was extensive exploitation of timber by the Portuguese colonial authorities, focussing primarily on *Pterocarpus angolensis* Harms (Umbila), *Azelia quanzenis* (Chanfuta), *Dalbergia melanoxylon* Guill. & Perr. (Pau-preto), *Milicia excelsa* (Welw.) C.C.Berg (Tule, Mvule), *Millettia stuhlmannii* Taub. (Jambiri, panga panga) and *Swartzia madagascariensis* Desv. (Pau-ferro), the effects of which can still be seen today (Timberlake et al. 2010).

Although many people moved out of rural areas during the independence struggle and civil war years (1960s to 1991), they are now starting to reoccupy many parts of the interior. This has been helped by better roads and transportation, including the construction of cut-lines during recent (2008) geophysical prospecting for oil, the sinking of wells and boreholes, and an influx of settlers from adjacent parts of Tanzania. The biggest threats to coastal forests at present are the rapid and uncontrolled clearance for subsistence agriculture, which is increasingly moving away from the main roads, logging (much of it illegal), and uncontrolled fires associated with settlement.

There is no formal protection of any coastal forest patches in Cabo Delgado except for a very small extent (less than 25 km²) inside the newly-proclaimed Quirimbas National Park. Given their characteristic features – the high turnover in species composition between patches, which often makes each patch unique, and the number of species with very restricted distributions – it is difficult to identify a ‘typical’ area for conservation protection or to cover the full range of important species in just a few areas.

Timberlake et al. (2010) have described fourteen areas of importance for conservation of coastal forests and associated vegetation types from across the study area. These cover the more diverse and intact areas identified so far and also various sites containing species of interest. Four sites (Pundahar–Nangade, Rio Macanga–Nhica do Rovuma, Quiterajo, Lupangua) are considered high priority. What is apparent is that in the northern parts along the Rovuma escarpment,

landscape-level conservation would be the most appropriate, covering dry forest, dense woodland, wooded grassland and the large seasonal pans – an ecosystem approach. This area is also a major source of water for coastal towns. Further south, where settlement is much denser, a site approach would be more appropriate, for example the raised plateau with *Guibourtia schliebenii* forest in the Quiterajo concession south of the Messalo River.

Current research at RBG Kew and IIAM, Maputo is attempting to identify Important Plant Areas across the broad study area. Once zoological findings from recent surveys are available it is planned to incorporate these in order to identify Key Biodiversity Areas. Such identified and documented areas will be brought to the attention of government and provincial authorities in Mozambique, who have already indicated interest in the study.

CONCLUSIONS AND FUTURE STUDIES

Although the area studied in detail was limited in extent, compounded by difficulties in access over much of it, some conclusions on the extent, distribution and biodiversity of coastal forests in northern Mozambique can be drawn.

1. Coastal forests similar to those in south-eastern Tanzania are present, but are far less extensive than had previously been suggested. The present extent of dry forest is around 400 km², although this may well be an over-estimate. Parts of this are now being rapidly cleared for agriculture.
2. Most of the forest patches seen are relatively small and confined to deeper, well-drained sandy soils, most apparently derived from the Mikindani sandstone formation. They are surrounded by woodland vegetation dominated by typical miombo species such as *Brachystegia*, other caesalpinoids and some Euphorbiaceae trees, species that (with the exception of the coastal *Berlinia orientalis*) are mostly very widely distributed across the sub-continent.
3. The forests generally comprise an upper canopy of deciduous species, many from the Caesalpinioideae (e.g. *Guibourtia schliebenii*, *Hymenaea verrucosa*, *Micklethwaitia carvalhoi*), with sclerophyllous evergreen species in the sub-canopy (e.g. *Manilkara* spp., *Warneckea sansibarica*, *Baphia macrocalyx*). The shrub layer is particularly rich in Rubiaceae. A surprisingly high proportion of these species have quite restricted ranges or are local endemics, being confined to parts of the coastal regions of southern Kenya, Tanzania and northern Mozambique. Many are confined to the Lindi–Mtwara–Cabo Delgado area, the so-called Lindi centre of endemism in the Swahilian regional centre of endemism (Clarke 1998, 2001). It is this attribute – the high proportion of range-restricted species – that gave rise to the discovery of so many new species and Mozambique records.
4. Despite the name, such coastal forests do not contain mesic evergreen species and show little similarity in composition or ecology to moist forests in the region, whether montane or lowland.
5. Another interesting feature is the high turn-over in species composition between forest patches. Most patches appear to be unique, and there is no species that is characteristic or found in most of them, the closest being *Pteleopsis*

myrtifolia (Combretaceae). Each patch appears to have a different dominant and suite of associates. This feature is either related to subtleties in the mineralogical or moisture status of the substrate, or could be solely an artefact of serendipity – the first species to arrive taking over.

6. The coastal forests are essentially ‘sand forests’ and, in many cases, show marked similarity in their structure, ecology and family (even generic) composition to areas of dry forest or thicket found on well-drained sandy soils across much of south-central Africa.
7. The high proportion of range-restricted species, the limited extent of the forest patches, and the increased threat, show that the coastal forests of northern Mozambique should be of international conservation concern. The possibilities of landscape or ecosystem-level conservation are now very limited, so attention also needs to be given to the selection of a range of sites across Cabo Delgado in order to conserve the full range of forest types and species.

The origins and affinities of these coastal dry forests, as well as determination of what the drivers for the marked levels of speciation and endemism might have been, remain important areas for research. But perhaps more urgent at this stage is continued documentation of the extent of coastal forests in other parts of Mozambique and the development of practical conservation measures needed to protect a rapidly disappearing vegetation type.

ACKNOWLEDGEMENTS

We would like to thank Pro Natura International and the Muséum National d’Histoire Naturelle, Paris, for organising the expeditions under their Our Plant Reviewed programme, and the Prince Albert II of Monaco Foundation, the Stavros Niarchos Foundation and the Total Foundation for funding. Much help in the field was given by Salim Annebi, Aurelio Banze, Sandie Burrows, Mervyn Lotter, Patricia Luke, Alice Massingue, Frédéric Mathias and Barbara Turpin. Field support and logistics during the expedition were ably provided by Mike Scott and his team from Khangela Safaris, Bulawayo, while Charlie Mackie provided aerial reconnaissance. We are particularly grateful to Iain Darbyshire and Tim Harris of the Drylands Africa team at RBG Kew for assistance in plant identification; Aaron Davis, Diane Bridson and the Rubiaceae team, Gill Challen, Martin Cheek, Anna Haigh, Ana-Claudia Araujo and Paul Wilkin also made valuable contributions. Erik Prins produced the satellite images and Justin Moat of the Kew GIS Unit helped prepare the maps. Neil Burgess and an anonymous reviewer made valuable comments on an earlier version of the paper.

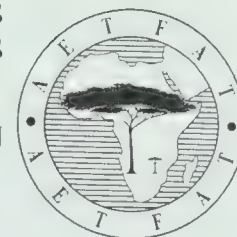
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Manuscript received 30 Sep. 2010; accepted in revised version 15 Feb. 2011. This paper was pre-published on 15 Jun. 2011 in issue 144(2) of *Plant Ecology and Evolution*.

Communicating Editor: Mats Thulin.



Structural and floristic typology of the forests in the forest-savanna mosaic of the Lopé National Park, Gabon

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Background and aims – The Lopé National Park in Gabon, recently added to the UNESCO world heritage list, presents a mosaic of forest and savanna that dynamically changes. Conserving this landscape requires an understanding of the forest dynamics. This study aims at defining a forest typology at Lopé in relation with its dynamics.

Methods – Floristic and structural characteristics for 265 tree species belonging to 55 families were measured in 258 sampling plots in the Lopé National Park. Multivariate analysis of these data was used to partition the sampling plots into groups on the basis of their floristic or structural characteristics.

Key results – Five structural forest types and six floristic forest types were identified. This typology showed that the forests in the forest-savanna mosaic of Lopé organize themselves along a gradient of forest recovery, from young forests to mature forests. Typical pioneer species are associated with the youngest forest stages. The gradient on the species also corresponds to a geographical gradient on the sampling plots, associated with features like altitude, rocks, or hydrography.

Conclusions – Five forest types were defined on the basis of species abundances. The snapshot of forest types characterizes a dynamic process of forest regeneration.

Key words – abundance, canopy height, floristic groups, forest type, forest-savanna mosaic, predominance, structural groups.

INTRODUCTION

Many tropical forests have once been disturbed by human activities, but after a long time following this disturbance, only a detailed examination of the structure and floristic composition of the vegetation can reveal a difference with pristine forests. The effect of selective logging on native tree diversity in tropical forests is a subject of speculation and of great current concern, but very limited data are available to assess its impact (Brown & Gurevitch 2004). Although certain genera of high commercial interest have been selectively logged, the structure of the forest is not easy to predict without analysing the forest as a dynamic system. Rain forest is a complex community whose framework is provided by trees of many

sizes. The consideration of the autoecology of individual tree species necessitates a reinterpretation of the much-discussed concept of stratification in the canopy (Whitmore 1975). The amount of new plant is low in the gap phase, increases to a maximum in the building phase, and declines during the mature phase. Patches of various sizes are the various phases of the forest growth cycle. The use of the stratification concept allows one discriminating species at different heights.

The dynamic nature of tropical forest can be illustrated by several changes (e.g. floristic composition), which means that different approaches are possible to analyse its structure after disturbance. One way is to analyze the size distribution of trees, or their stratification (Hallé et al. 1978). The forest

is made up of a vast number of units interacting with each other. Despite that temperate forests are usually taken as examples to understand results in rain forests, basic concepts like tree height-diameter relationships (Schulz 1960) can be useful to understand the contrast of trees in closed and open environment, in relation with the vertical forest structure. To assess the role of a floristic community as a building element of the forest, the growth potential of tree species can be analysed (Hallé et al. 1978). Architecture indicates the population characteristics of forests and the change from one phase to another.

The tropical rain forest is no longer considered as a homogeneous entity, but rather as an heterogeneous ensemble of units with different ages, compositions, structures, and sizes (Aubréville 1938, Riéra et al. 1998). The silvatic mosaic and the stratification concept (Oldeman 1990) provide architectural criteria to analyse the organization of a forest system. When studying the vertical structure of forests, height classes can be defined together with groups of species with different height growth potential (Schulz 1960). Quoting Hallé et al. (1978), “in the vertically successive structural ensembles there is a mosaic of crowns shadowed by those above them. This systematic segregation may be taken as an indication that different species can achieve maximum photosynthetic activity under different light regimes”. The characterization of vegetation groups relies on the most significant variables such as the number of individuals, their size, and their spatial distribution (Schulz 1960). Disturbances are phenomena that contribute to the structuring of the ecosystems. The intermediate disturbance hypothesis (Connell 1978) predicts a maximum species richness for intermediate disturbance frequencies and intensities. Two conceptual models explain the renewal of vegetation types: species replacements along the phases of succession, or species outbreaks in varying proportions depending on the time of forest reconstitution (Clements 1916, Lepart & Escarré 1983).

In this study, available data from sampling plots surveyed in different vegetation formations in the Lopé National Park in Gabon, taking account of the history of selective logging (White 1996), was used to identify the characteristics of vegetation formations following disturbance. Multivariate analyses (PCA, CA, CCA) were used to test the hypothesis that human induced disturbances influence the floristic composition and the structure of vegetation formations. These results on the vegetation types in relation to disturbance are essential to implement conservation strategies in the National Park. This study thus addresses the two following questions: (i) What are the relevant structural and floristic variables to identify vegetation types in the Lopé National Park? (ii) Is the current forest pattern at Lopé an outcome of the interplay between the forest-savanna mosaic and recent disturbances? The relationship between forest structure and its floristic composition was analysed on the basis of species abundances in sampling plots.

MATERIAL AND METHODS

Study site and sampling design

Research was carried out in the Lopé National Park, central Gabon (0°4'S 11°44'E). Our study site concerned the 300

km² of savanna and forest-savanna mosaic along the northern and eastern limits of the park. Lopé has the lowest rainfall in Gabon (M.E.N. 1983). The mean annual rainfall taken at the SEGC research station in the centre of the study site is 1474 mm (SE $\pm$ 44.8, from 1984 to 2004). There is a marked seasonality in the distribution of rainfall, with a long dry season between mid-June and mid-September whose severity and duration varies between years. A shorter and more variable dry season also occurs around January and February. Lopé's comparatively low rainfall is due to a rain shadow effect from the Massif du Chaillu mountains southwest of Lopé NP, and a low band of rainfall associated with the Ogooué river (White 2007). Temperature varies little throughout the year, although it is slightly cooler in the long dry season due to an almost constant cloud cover. A temperature logger placed in the open savanna at the SEGC research station recorded an overall mean daily temperature of 25.9°C (SE $\pm$ 0.06 from January 2003 to December 2004), with temperatures ranging from 17.5°–38.8°C throughout this period.

The relief consists to the South of a chain of convex hills dominated by the Okanda chain (450–850 m in height). This chain continues to the South where it reaches its highest point of about 900 m. The North part is a former lake basin that was opened when the Ogooué river went through the Okanda chain. Erosion is strong on the slopes (UNESCO 2006). Vegetation in Lopé is a complex mosaic of plants association (White 1992). Three main forest types can be distinguished: gallery forests and bosques within the forest-savanna mosaic; young forests; and mature forests.

Available data collected at Lopé for different purposes were used in this study. Although the resulting sampling design was not optimal for our study, we ensured that this did not result in biased estimate of vegetation characteristics. The sampling design consisted of two types of sampling units: plots and transects. Plots were 800 m² in area (20 m $\times$ 40 m). All the trees with a diameter at breast height (dbh) greater than 10 cm were inventoried in the plots. Their diameter and height were measured, and their species was identified. In total, 103 plots (totalling 8.24 ha) containing 3630 trees with dbh $\geq$ 10 cm and 195 distinct species were inventoried between 1983 and 2008. Each plot was inventoried once (no longitudinal monitoring). Transects were 5 km long and their width depended on the dbh of the trees: trees with 10 $\leq$ dbh < 70 cm were inventoried as far as 2.5 m from the transect line (thus a width of 5 m), whereas trees with dbh $\geq$ 70 cm were inventoried as far as 25 m from the transect line (thus a width of 50 m). Like for the plots, diameter and height of every inventoried tree were measured, and their species was identified. The location of each tree along the transect (distance since the origin of the transect) was also measured. In total, 5 transects (totalling 12.5 ha for dbh < 70 cm and 62.5 ha for dbh $\geq$ 70 cm) containing 5175 trees and 182 distinct species were inventoried between 1989 and 2008.

A visual inspection of satellite images enabled us to classify the sampling units according to the main forest types. Young forests and mature forests could not be visually discriminated on satellite images, and were thus jointly classified as continuous forest. Plots were distributed as 28% in continuous forest, 27% in gallery forest, and 45% in bosques and savannas. Transects were all located in continuous forest.

Four transects were located in formerly logged forest, while one transect (n°5) was located in unlogged forest.

Floristic and structural data

To jointly analyse plot and transect data, we first converted transects into plots by truncating each 5 km long transect into 31 sections, each 160×5 m. Thus, plots and transect sections had the same area (800 m^2), but not the same shape. As plot shape impacts the precision of estimation of the sampled quantities but not their expectation (e.g. Bormann 1953), differences in plot shapes have little influence in this study. Weighted means were used to correct for the variable width of the transects, as specified below. Two data sets were built from individual tree measurements in plots and transects: the floristic and the structural data set. Each data set had 258 rows that corresponded to the 258 sampling units (103 plots + 155 transect sections).

The floristic data set gave the abundance of each species in each sampling unit. For transect sections, the abundance N_s of a focal species s in 800 m^2 was computed as: $N_s = N_{<70,s} + N_{\geq 70,s}/10$, where $N_{<70,s}$ is the abundance of trees with dbh < 70 cm of species s in the 160×5 m transect section, whereas $N_{\geq 70,s}$ is the abundance of trees with dbh ≥ 70 cm of species s in the 160×50 m transect section. The total number of distinct species found in plots and transects was 265, thus resulting in 265 columns for the floristic data set.

The structural data set reported on 12 structural variables for each sampling unit: (1) total tree abundance N , that is the number of trees in 800 m^2 ; (2) total basal area B in 800 m^2 , computed as:

$$B = (\pi/4) \sum_{i=1}^6 D_i^2$$

where D_i is the diameter of the i th tree of the sampling unit; (3)–(8) tree abundances N_i in 6 diameter classes, where N_i ($i = 1, \dots, 5$) is the number of trees with $5 + (i - 1) \times 10 \text{ cm} < \text{dbh} \leq 5 + i \times 10 \text{ cm}$, and N_6 is the number of trees with dbh $> 55 \text{ cm}$ (hence $\sum_{i=1}^6 N_i = N$); (9) mean height $\bar{H}$ within the 800 m^2 sampling unit; (10) standard deviation σ_H of height within the 800 m^2 sampling unit; (11) maximal height $H_{\max}$; (12) identity of the species that has the maximal height within the 800 m^2 sampling unit.

As transects had variable width, estimates derived from transect data had to be adjusted using varying size sampling estimators. The adjustment was not the same for cumulative estimates (such as tree density or basal area), for estimated means (such as mean height), and for estimated standard deviations. Hence three types of estimators were used. The estimator of a cumulative quantity X in a transect section was:

$$X = X_{<70} + X_{\geq 70}/10 \quad (1)$$

where $X \equiv N, N_i$ or B , $X_{<70}$ was the value of X when restricting to trees with dbh < 70 cm in the 160×5 m transect section, and $X_{\geq 70}$ was the value of X when restricting to trees with dbh ≥ 70 cm in the 160×50 m transect section. Mean values in transect sections were estimated as:

$$\bar{X} = \frac{1}{N_{<70} + N_{\geq 70}/10} (N_{<70} X_{<70} + N_{\geq 70} X_{\geq 70}/10) \quad (2)$$

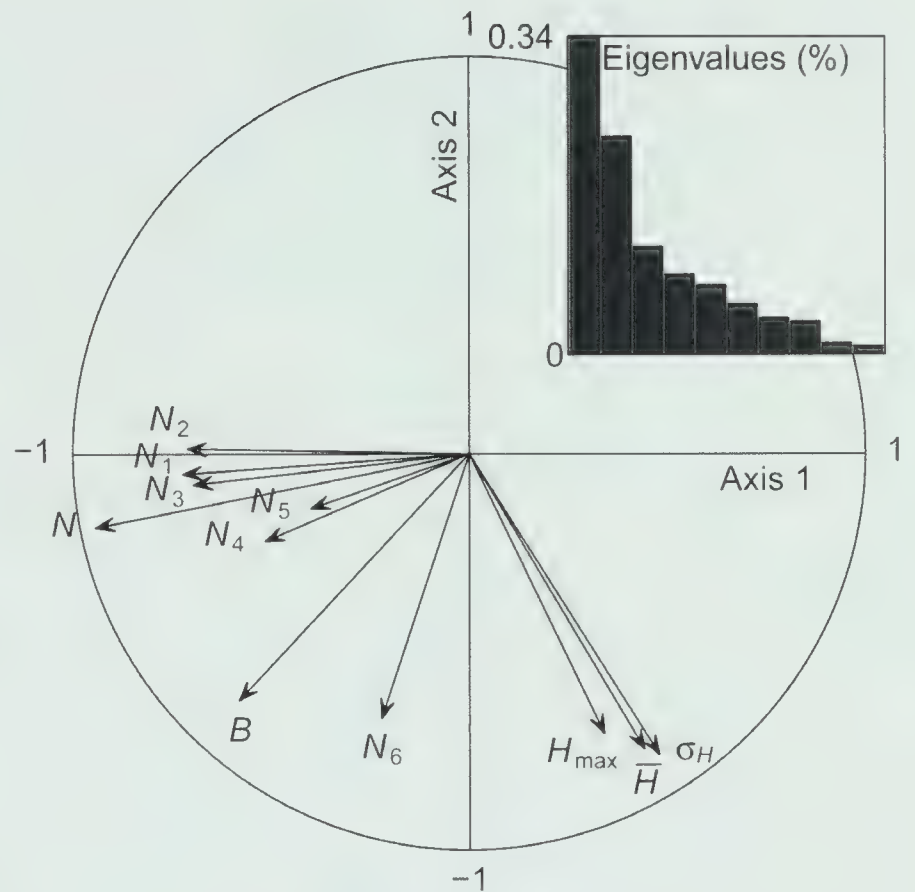


Figure 1 – Correlation circle of the principal component analysis of the structural variables for 258 sample plots at Lopé, Gabon. N_i is the number of trees in the i th diameter class, N is the total number of trees, B is basal area, $\bar{H}$ is mean height, $H_{\max}$ is maximal height, and σ_H is the standard deviation of height.

where X was height H (so that $\bar{X} \equiv \bar{H}$ was mean height) or square height H^2 (so that $\bar{X} \equiv \bar{H}^2$ was mean square height), $X_{<70}$ was the mean of X when restricting to trees with dbh < 70 cm in the 160×5 m transect section, and $X_{\geq 70}$ was the mean of X when restricting to trees with dbh ≥ 70 cm in the 160×50 m transect section. The standard deviation of height for transect sections was estimated as:

$$\sigma_H = \sqrt{\bar{H}^2 - \bar{H}^2} \quad (3)$$

where mean height $\bar{H}$ and mean square height $\bar{H}^2$ were computed using (2). We checked that estimators (1)–(3) when applied to transect data did not bring any noticeable bias by comparing the distribution of each structural variable in plots and in transect sections. Similar distributions were indeed obtained. The structural data set thus had 12 columns.

Multivariate analyses

Analyses of structural data – Structural variables were analyzed using a principal component analysis (PCA) of the 258×11 matrix giving the eleven quantitative structural variables for each sampling unit (Härdle & Simar 2003, chapter 9). The PCA was complemented with a hierarchical cluster analysis to partition the 258 sampling plots into groups (Härdle & Simar 2003, chapter 11). This cluster analysis used the Euclidean metric to measure differences between plots and Ward's method to cluster groups (Ward 1963). As these groups of plots were based on structural variables, we hereafter call them the 'structural groups'. Mean values of the structural variables for each structural group were computed.

Table 1 – Mean values of the structural variables for each group of plots.

The groups were defined from structural variables. N_i is the number of trees in the i th diameter class, N is the total number of trees, B is basal area, $\overline{H}$ is mean height, $H_{\max}$ is maximal height, σ_H is the standard deviation of height, CI is Clapham index.

structural variable	unit	structural group				
		1	2	3	4	5
N_1	ha ⁻¹	108.7	117.3	152.9	142.1	415.6
N_2	ha ⁻¹	96.0	83.2	101.9	151.0	241.7
N_3	ha ⁻¹	45.0	40.7	51.9	69.2	133.3
N_4	ha ⁻¹	27.5	31.6	38.5	33.8	75.0
N_5	ha ⁻¹	11.2	18.6	8.2	30.1	37.5
N_6	ha ⁻¹	18.9	50.8	27.4	23.0	55.2
N	ha ⁻¹	307.2	342.1	380.8	449.1	958.3
B	m ² ha ⁻¹	20.3	38.8	28.8	29.2	57.6
$\overline{H}$	m	15.6	20.5	11.4	15.6	13.3
$H_{\max}$	m	37.8	41.5	19.7	32.9	30.5
σ_H	m	7.8	10.2	4.7	7.7	6.1
CI		2.1	3.3	3.7	2.3	2.7

The description of structural groups was complemented with two additional descriptors, not included in the PCA. First, the distribution of the species with the maximal height within each plot was computed for each group. These are the species that form the canopy. Second, Clapham index was computed for each structural group from the counts of trees in each plot (Pielou 1969). If n_k is the number of plots in group k , and N_{jk} ($j = 1, \dots, n_k$) is the number of trees in the j th plot of group k , Clapham index (CI) for group k is defined as the empirical variance of $N_{1k}, \dots, N_{n_k k}$ divided by its mean. If N_{jk} is distributed as a Poisson variable, then CI equals one. Clapham index thus is a rough index to characterize the spatial pattern of trees, where over-dispersion with respect to the Poisson distribution ($CI > 1$) means that trees have a clustered spatial pattern, whereas under-dispersion with respect to the Poisson distribution ($CI < 1$) means that trees have a regular spatial pattern. Departure from the null hypothesis of random spatial pattern ($CI = 1$) was tested using a Monte Carlo test with CI as the test statistic.

The relationship between the structural groups and the type of sampling unit (either a plot or a part of the 1st, 2nd, ..., 5th transect) was tested using a χ^2 test. The relationship between the structural groups and the main forest types (bosque, gallery forest, continuous forest) was also tested using a χ^2 test.

Analyses of floristic data – Floristic data were analyzed using a correspondence analysis (CA) of the 258×265 table giving the abundance of each species in each sampling unit (Härdle & Simar 2003, chapter 13). The same analysis was repeated after collapsing the species abundances into family abundances. As the 265 species belonged to 55 distinct families, a 258×55 table of family abundances in each sampling unit was analyzed.

The CA was complemented with a hierarchical cluster analysis to partition the 258 sampling plots into groups. This cluster analysis used the Euclidean distance between plots in

the plane formed by the first two axes of the CA, and Ward's method to cluster groups. As these groups of plots were based on floristic variables, we hereafter call them the 'floristic groups'.

The relationship between the floristic groups and the type of sampling unit (either a plot or a part of the 1st, 2nd, ..., 5th transect) was tested using a χ^2 test. The relationship between the floristic groups and the main forest types (bosque, gallery forest, continuous forest) was also tested using a χ^2 test.

Relationship between structural and floristic data – The relationship between structural and floristic data was first investigated using a canonical correspondence analysis (CCA) of the pair of tables, one giving the abundance of each species, and the other giving the structural variables in each sampling unit. CCA consists in replacing the observed abundance A_s of species s in a given plot by its abundance predicted by the multiple regression on structural variables: $A_s = a_s + \varepsilon_s$, where ε_s is the residual error,

$$a_s = \beta_{0s} + \sum_{i=1}^6 \beta_{is} N_i + \beta_{7s} N + \beta_{8s} B + \beta_{9s} \overline{H} + \beta_{10s} H_{\max} + \beta_{11s} \sigma_H$$

and the β_{is} ($i = 1, \dots, 11$) are the estimated regression coefficients. Then a correspondence analysis on the table of predicted abundances a_s is performed (Couteron et al. 2003). The inertia of the table of predicted abundances a_s can be compared to the inertia of the table of observed abundances A_s . Moreover, we can test if the former is significantly different from zero using a Monte Carlo test based on random permutations of the table rows (Couteron et al. 2003).

Second, a χ^2 test was performed on the contingency table that cross-tabulates the 258 sampling units between structural groups and floristic groups, to test for the relationship between these two groupings. Analyses of variance of the structural variables with respect to the floristic groups were conducted to test for differences in structural variables between floristic groups. Conversely, analyses of variance of the species abundances with respect to the structural groups

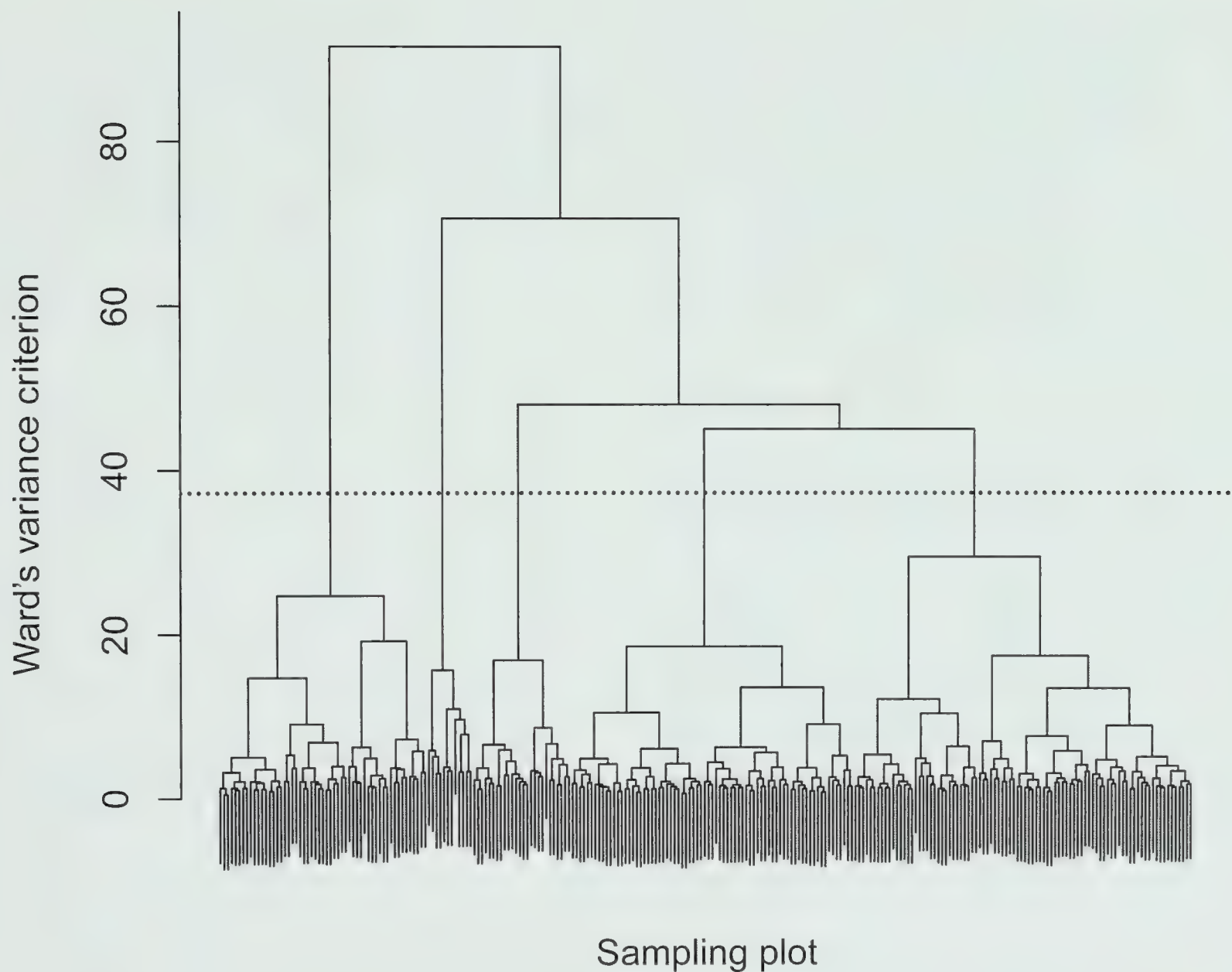


Figure 2 – Dendrogram of the hierarchical cluster analysis of the 258 sample plots at Lopé, Gabon on the basis of their structural variables. The dotted line shows where the dendrogram was cut to define the structural groups.

were conducted to test for differences in species abundances between structural groups.

Additional multivariate analyses of floristic and structural data were performed but are not reported here since they brought little additional information. They can be found as supplementary data.

RESULTS

Structural characteristics

Two groups of positively correlated variables were shown up by the PCA of structural variables (fig. 1). The first group gathers N and N_1 - N_4 and explains the first axis of the PCA. It thus corresponds to tree density, with the strongest contribution to the total density of the smallest diameter classes. The second group gathers the variables related to height ($\bar{H}$, $H_{\max}$, and σ_H) and explains the second axis of the PCA. It thus corresponds to the height of the canopy. Variables B and N_6 , that are positively correlated, stand in between: large basal areas are found when the plots contain many large trees, and many large trees also means a high canopy. The dendrogram of the hierarchical cluster analysis on structural variables (fig. 2) suggested to partition the 258 sampling units into five groups. Whatever the group, Clapham index was significantly greater than one (table 1), with p -values always less than 1%.

Hence, the spatial pattern of trees was always significantly clustered at the scale of 800 m². Using the mean values of the structural variables (table 1), the structural groups could be interpreted as follows:

Group 1 – It gathers 75 sampling units, and is characterized by the lowest density (whether one considers the total density or the density per class) and the lowest basal area. Canopy height is medium, and spatial clustering is the weakest. The plots of this group thus are low-density plots. The species that form the canopy are varied (23 distinct species), with a dominance of *Aucoumea klaineana* Pierre (18.8% of the plots), *Dacryodes buettneri* (Engl.) H.J.Lam (16.7%), and *Lophira alata* Banks ex Gaertn. (10.4%).

Group 2 – It gathers 55 sampling units, and is characterized by the highest canopy height (whether one considers mean height, maximum height, or height standard deviation). It has few trees in the lowest diameter classes (N_1 - N_3), but many trees in the largest diameter class (N_6), and a quite elevated basal area, thus resulting in the highest ratio of basal area over tree density. The plots of this group thus are low-density plots but with the presence of large trees with a high canopy. The canopy species do not vary much (thirteen species), with an overwhelming dominance of *Aucoumea klaineana* Pierre (48.9% of the plots; the second commonest species being *Pterocarpus soyauxii* Taub. with 13.3%).

Table 2 – Analysis of variance of the structural variables with respect to the floristic groups at Lopé, Gabon.

Letters indicate the different levels according to Tukey’s multiple paired comparison test. N_i is the number of trees in the i th diameter class, N is the total number of trees, B is basal area, $\overline{H}$ is mean height, $H_{\max}$ is maximal height, and σ_H is the standard deviation of height.

structural variable	unit	mean value within floristic group						F	p-value
		1	2	3	4	5	6		
N_1	ha ⁻¹	157.9 ^b	135.8 ^{ab}	156.8 ^{ab}	111.5 ^a	148.8 ^{ab}	250 ^{ab}	2.73	0.02
N_2	ha ⁻¹	110.9 ^a	100.6 ^a	121.6 ^{ab}	122.9 ^{ab}	154.1 ^{bc}	258.3 ^c	7.27	< 0.001
N_3	ha ⁻¹	54.1 ^a	48.3 ^a	80.7 ^a	58.1 ^a	64.1 ^a	150 ^b	6.19	< 0.001
N_4	ha ⁻¹	35.5	32.5	34.1	33.3	30.6	75	1.76	0.123
N_5	ha ⁻¹	18.4	21.1	17	20.8	20.3	50	1.74	0.125
N_6	ha ⁻¹	31.9 ^a	36.6 ^a	42 ^{ab}	24.5 ^{ab}	17.1 ^b	41.7 ^{ab}	4.17	0.001
N	ha ⁻¹	408.7 ^a	375 ^a	452.3 ^a	371.2 ^a	434.9 ^a	825 ^b	4.92	< 0.001
B	m ² ha ⁻¹	33.1 ^{ab}	31 ^{ab}	34.1 ^{ab}	26.2 ^a	24.9 ^a	54.2 ^b	4.34	0.001
$\overline{H}$	m	14.6 ^b	18.7 ^a	11.6 ^b	15.5 ^b	15.1 ^b	12.8 ^{ab}	11.71	< 0.001
$H_{\max}$	m	27.9 ^c	38.8 ^a	24.5 ^{bc}	37.9 ^a	36.3 ^{ab}	21 ^{abc}	11.28	< 0.001
σ_H	m	6.5 ^c	9.4 ^a	5.6 ^{bc}	8 ^b	7.7 ^{bc}	4.3 ^{abc}	12.08	< 0.001

Group 3 – It gathers 26 sampling units, and is characterized by the lowest canopy height (whether one considers mean height, maximum height, or height standard deviation). Its tree density is medium (whether one considers the total density or the density per class), and its basal area is medium as well. Spatial clustering is the strongest. The canopy species are dominated by *Lophira alata* Banks ex Gaertn. (16.0% of the plots) and *Craibia laurentii* De Wild. (12.0%), for a total of eighteen distinct species.

Group 4 – It is the largest group with ninety sampling units, but is also the group without any specific feature: all struc-

tural variables take medium values. The canopy species are varied (28 distinct species), with a dominance of *Aucoumea klaineana* Pierre (23.6% of the plots), *Dacryodes buettneri* (Engl.) H.J.Lam (7.3%), and *Lophira alata* Banks ex Gaertn. (7.3%), which are the same species than in group 1.

Group 5 – It gathers twelve plots, and is characterized by the highest density (whether one considers the total density or the density per class) and the highest basal area. Canopy height is medium. The plots of this group thus are high-density plots. The species that form the canopy are limited to seven species, with a dominance of *Hylodendron gabunense* Taub. (30% of the plots) and *Aucoumea klaineana* Pierre (20% of the plots). The structural groups turned out to be significantly related to the type of sampling unit ($\chi^2 = 225.0$, p -value < 0.001): structural group 2 was strongly associated with transect 2, group 3 was associated with plots, and group 4 was weakly associated with transect 4. The structural groups were also significantly related to the main forest types ($\chi^2 = 111.9$, p -value < 0.001): structural groups 3 and 5 were jointly associated with bosques and gallery forests, but continuous forest did not show any specific relation to any structural group.

Floristic characteristics

The CA of species abundances presented a Guttman effect (fig. 3) that denoted a gradient along the first axis of the CA. The most abundant species (*Cola lizae* N.Hallé, *Santiria trimera* (Oliv.) Aubrév., *Aucoumea klaineana* Pierre, *Lophira alata* Banks ex Gaertn.) were found at the centre of this gradient, the extremities of the gradient being occupied by species that were globally rare but locally abundant in some sampling units.

The dendrogram of the hierarchical cluster analysis on species abundances (fig. 4) suggested to divide the 258 sampling units into six floristic groups. These floristic groups ordered along the gradient corresponding to the first axis of the CA (fig. 3). The floristic groups were significantly related to the type of sampling unit ($\chi^2 = 343.4$, p -value < 0.001). Plots were associated with floristic groups 1, 3 and 6, which

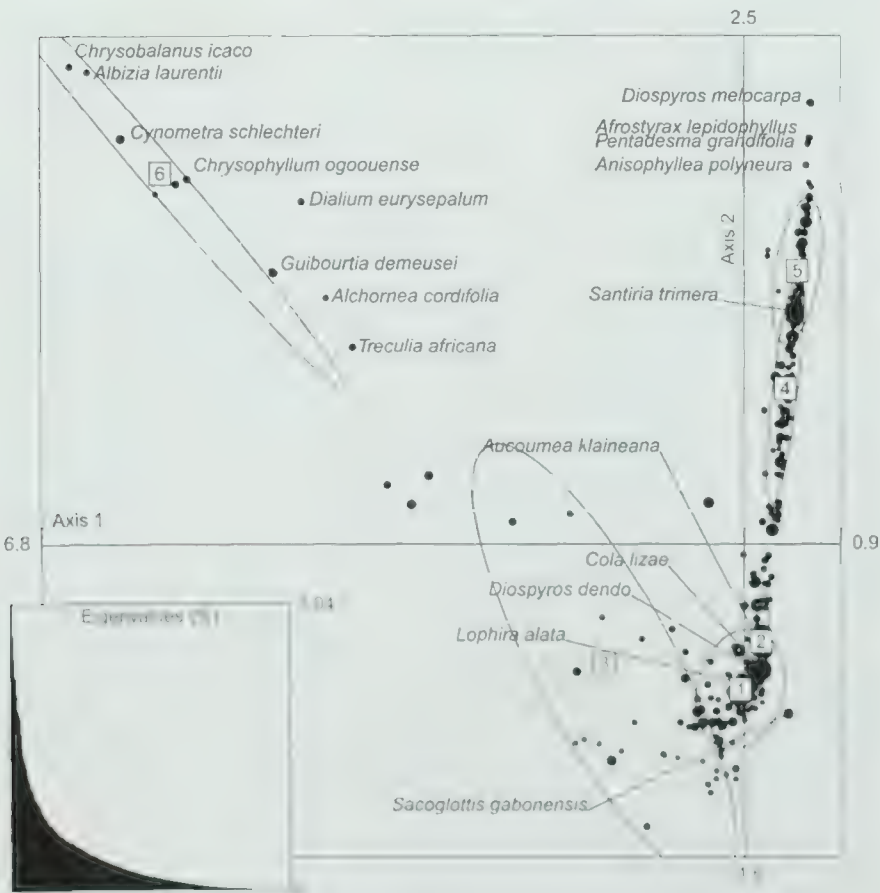


Figure 3 – Projection of species (dots) and of floristic groups (ellipses) on the first two axes of the correspondence analysis of the species abundances at Lopé, Gabon. The size of dots is proportional to the square root of species abundances.

corresponded to the left-hand side of the gradient. Transects 1 and 2 were almost exclusively found in floristic group 2 (at the centre of the gradient), whereas transects 3–5 were almost exclusively found in floristic groups 4 and 5 (to the right-hand side of the gradient). The gradient of the CA thus corresponded to a geographical gradient of forest types, from plots to transects 3–5 through transects 1 and 2 (fig. 5).

The floristic groups were also significantly related to the main forest types ($\chi^2 = 198.0$, $p\text{-value} < 0.001$): floristic group 1 was strongly associated with bosques, floristic groups 3 and 6 were strongly associated with gallery forests, while continuous forest did not show any specific relation to any floristic group.

When analyzing family abundances rather than species abundances, a strong opposition was found between the Humiriaceae on the one hand, and all other families on the other hand. At Lopé, the Humiriaceae were represented by a single species, *Sacoglottis gabonensis* (Baill.) Urb. This species was located in the middle of the gradient of the CA (fig. 3). It was globally rare (it was found in fifteen sampling units out of 258) but, when it was found, it was abundant.

Relationship between structural and floristic characteristics

When performing the CCA, the total inertia of the table of predicted abundances was 1.44, to be compared to 21.3 for the table of observed abundances. Yet this value was significantly different than zero ($p\text{-value} < 0.001$), thus indicating a significant relationship between the structural variables and the floristic characteristics. The correlation circle of the CCA was similar, up to a rotation, to the correlation circle of the PCA (fig. 6). The first axis of the CCA was positively correlated with density and negatively correlated with canopy height. Its second axis discriminated dense plots with a high canopy from low-density plots with a low canopy. The projection of species on the first two axes of the CCA was very different from their projection on the first two axes of the CA, thus indicating that the gradient along the first axis of the CA could not be explained by structural variables (fig. 7). The most abundant species (*Cola lizae* N.Hallé, *Santiria trimera* (Oliv.) Aubrév., *Aucoumea klaineana* Pierre, *Lophira alata* Banks ex Gaertn.) were found in the left part of figure 7. They were thus predominantly found in low-density plots with a high canopy, which corresponds to the description of structural group 2.

Structural groups and floristic groups were significantly related ($\chi^2 = 148.5$, $p\text{-value} < 0.001$). A correspondence was found between structural groups 5, 2, 3 and floristic groups 6, 2, 1, respectively. A weaker correspondence was also found between structural groups 1, 3, 4 and floristic groups 4, 3, 5

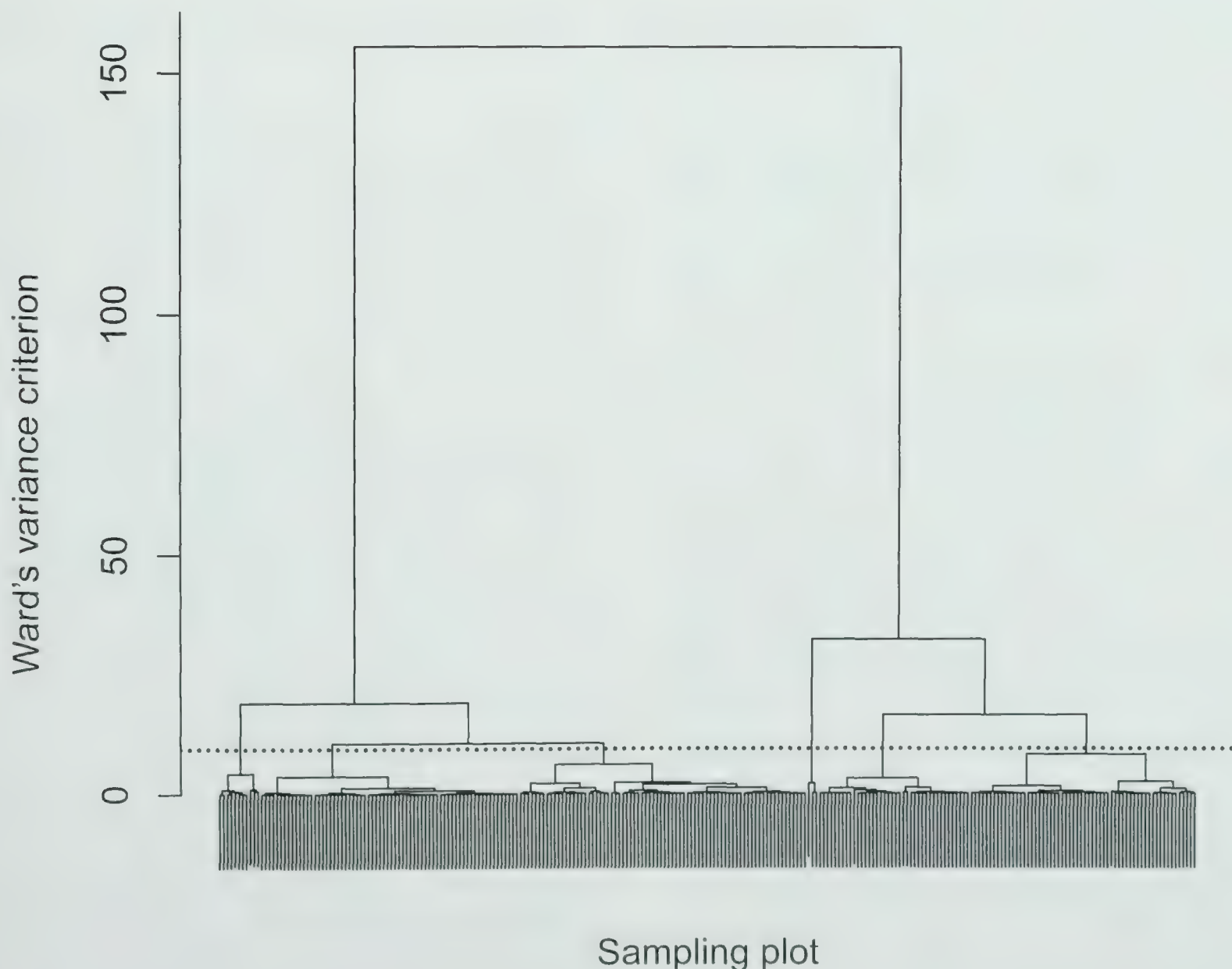


Figure 4 – Dendrogram of the hierarchical cluster analysis of the 258 sample plots at Lopé, Gabon on the basis of their species abundances. The dotted line shows where the dendrogram was cut to define the floristic groups.

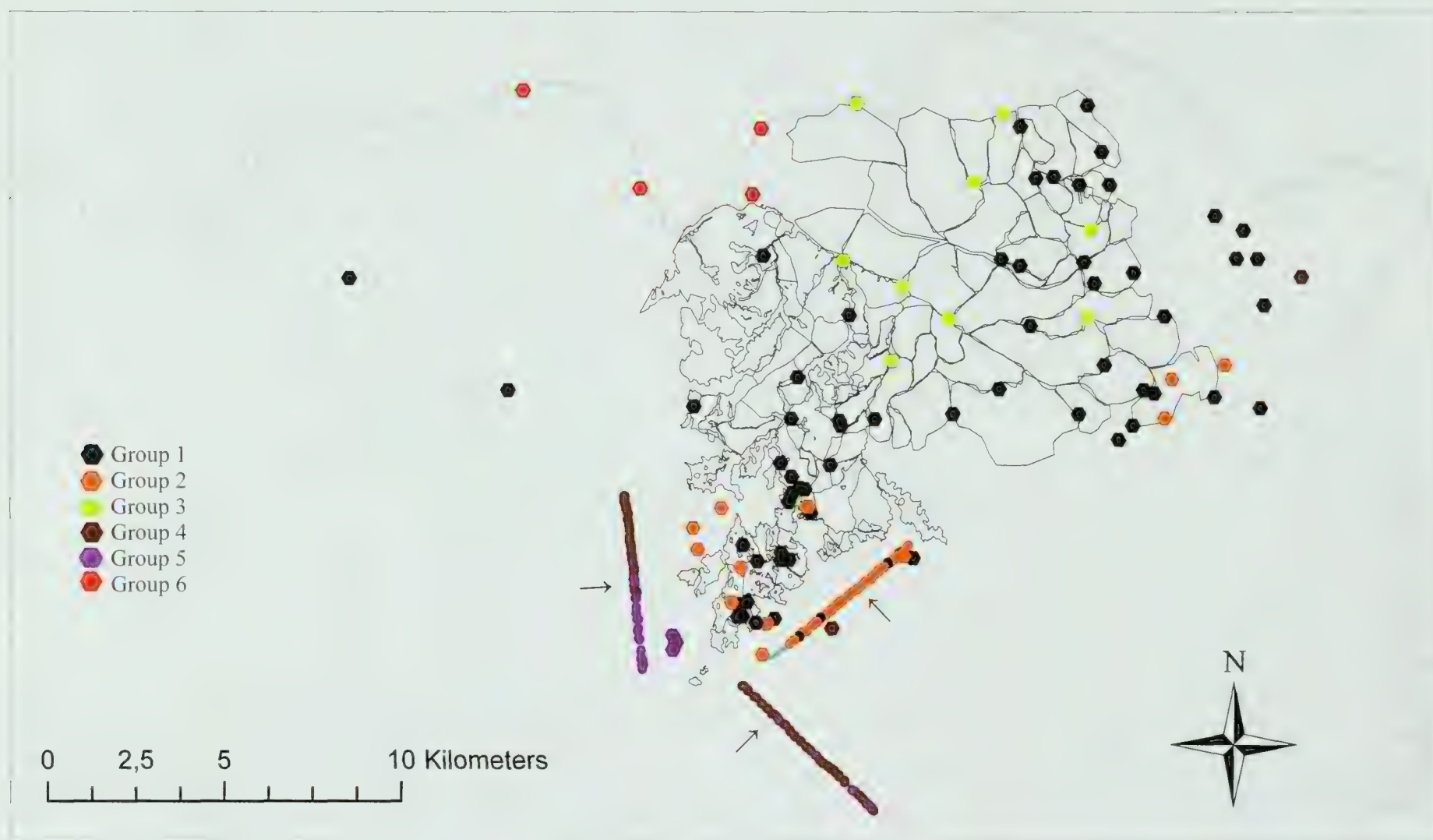


Figure 5 – Location of the sampling plots in the Lopé National Park, Gabon, together with the six floristic groups to which they belong. In grey: Lopé National Park border; in black: savanna border; arrows indicates the three transects.

respectively. These correspondences were consistent with the associations previously identified between either structural or floristic groups and the type of sampling unit. For instance, structural group 2 was associated with transect 2, and corresponded to floristic group 2 that was also associated with transect 2.

With the exception of N_4 and N_5 , all structural variables were significantly different between floristic groups (table 2). As the correspondence between structural groups and floristic groups was not perfect, the structural characteristics of the floristic groups were not as contrasted as those of the structural groups. Yet some agreement was found between the structural characteristics of the two groupings. For instance, floristic group 2 was characterized by a low density and a large canopy height (table 2), in the same way as structural group 2 (table 1) to which it was associated. Another example is floristic group 6 that was characterized by a high density and a large basal area (table 2), in the same way as structural group 5 (table 1) to which it was associated.

Among the 265 species found at Lopé, 82 had significantly different abundances between the five structural groups at 5% level. This enabled us identifying the species specific to each structural group. Thus, the description of the structural groups given before could be complemented with the following floristic information:

- Group 1 had *Desbordesia glaucescens* (Engl.) Tiegh., *Dialium guineense* Willd., *Carapa procera* DC., *Grewia coriacea* Mast., and *Scyphocephalum mannii* (Benth.) Warb. as characteristic species.

- Group 2 had *Cola lizae* N.Hallé, *Aucoumea klaineana* Pierre, *Lophira alata* Banks ex Gaertn., *Diospyros polystemon* Gürke, *Xylopia hypolampra* Mildbr., *Hypodaphnis zenkeri* (Engl.) Stapf, and *Berlinia bracteosa* Benth. as characteristic species. This result had already been partially given by the CCA.
- Group 3 had *Uapaca guineensis* Müll.Arg, *Craibia laurentii* De Wild., *Paropsia grewioides* Welw. ex Mast., *Pseudospondias microcarpa* (A.Rich.) Engl. var, *Milicia excelsa* (Welw.) C.C.Berg, *Aidia ochroleuca* (K.Schum.) E.M.A.Petit, *Detarium macrocarpum* Harms, and *Chytranthus talbotii* (Baker f.) Keay as characteristic species.
- Group 4 had *Santiria trimera* (Oliv.) Aubrév., *Centroplass glaucinus* Pierre, *Strombosiopsis tetrandra* Engl., *Dacryodes klaineana* (Pierre) H.J.Lam, and *Coula edulis* Baill. as characteristic species.
- Group 5 had *Diospyros dendo* Welw. ex Hiern, *Pentaclethra eetveldeana* De Wild. & T.Durand, *Diospyros zenkeri* (Gürke) F.White, *Diospyros iturensis* (Gürke) Letouzey & F.White, *Xylopia aethiopica* (Dunal) A.Rich., *Guibourtia demeusei* (Harms) J.Léonard, *Cynometra schlechteri* Harms, *Dialium lopense* Breteler, *Antidesma vogelianum* Müll.Arg, *Pachystela brevipes* (Baker) Baill. ex Engl., *Aphanocalyx djumaensis* (De Wild.) J.Léonard, *Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill., *Baikiaea robynsii* Ghesq. ex Laing, *Ongokea gore* (Hua) Pierre, *Elaeis guineensis* Jacq., *Cathormion altissimum* (Hook.f.) Hutch. & Dandy, *Dialium eurysepalum* Harms,

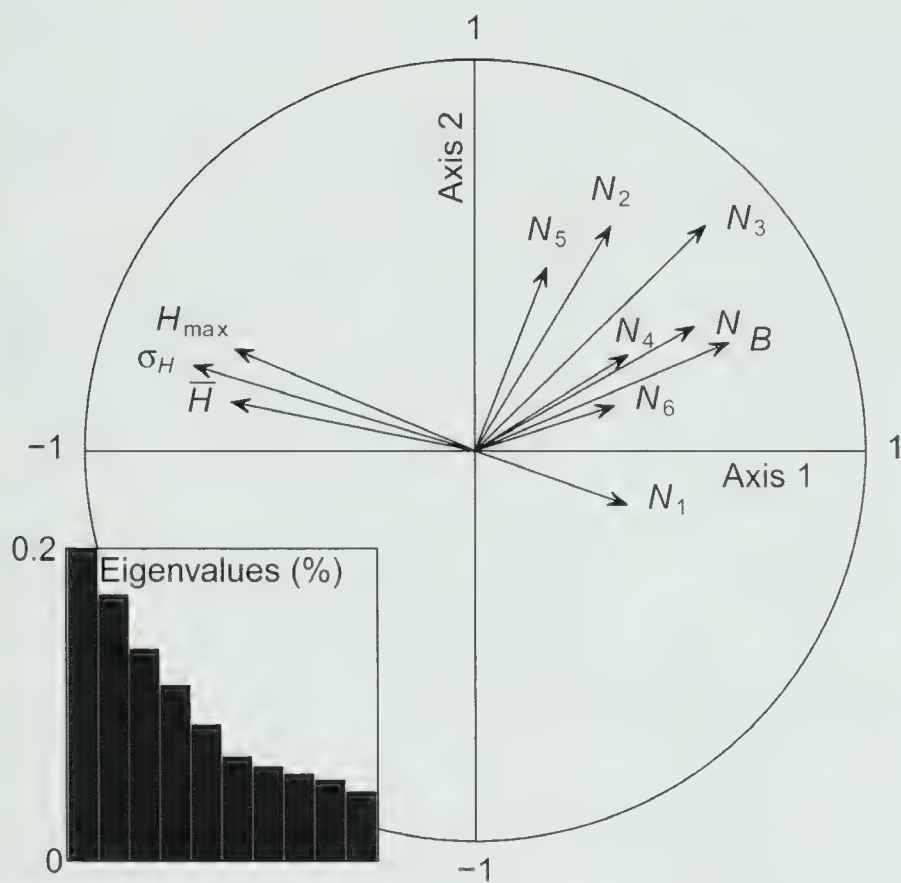


Figure 6 – Correlations between the structural variables and the first two axes of the canonical correspondence analysis of the species abundances at Lopé, Gabon. N_i is the number of trees in the i th diameter class, N is the total number of trees, B is basal area, $\bar{H}$ is mean height, $H_{\max}$ is maximal height, and σ_H is the standard deviation of height.

Psychotria venosa (Hiern) E.M.A.Petit, *Vitex doniana* Sweet, *Pycnanthus angolensis* (Welw.) Warb., *Connarus griffonianus* Baill., *Ficus subsagittifolia* Mildbr. ex C.C.Berg, *Holarrhena floribunda* (G.Don) Dur. & Schinz, *Millettia griffoniana* Baill., *Monanthotaxis klainei* (Pierre ex Engl. & Diels) Verdc., *Oxyanthus unilocularis* Hiern, *Rothmannia whitfieldii* (Lindl.) Dandy, and *Uapaca heudelotii* Baill. as characteristic species.

DISCUSSION

Vegetation at Lopé could be classified into five or six types depending on whether these types were defined from structural or floristic characteristics. Although structural and floristic groups were significantly related, they reflected different information. In particular, floristic groups were ordered along a gradient that could not be explained by structural variables. When using a classification method based on floristic data with a weight for each species proportional to its abundance, this gradient vanishes and floristic groups become more similar to structural groups.

Structural characteristics

In terms of tree density, a strong opposition was found between the many individuals in the young stages and those of the highest diameter classes. The significant relationship between the number of trees in diameter class N_6 and basal area suggests that the corresponding species are commercial species that were not removed following selective logging. The species that reach a large diameter identify with those that

are dominant in the canopy, in terms of basal area, height, or abundance. As these species are also the ones that are found in the plots with the highest basal areas, we can conclude that both basal and density are indicators of the structure of the vegetation groups in our study. These results contrast with those of Schulz (1960) regarding the weight of basal area: “I am not sure that its classificatory value is really greater than that of the number of individuals” wrote Schulz when he described the floristic composition of Mapane forest.

In terms of height, an opposition was found between the plots with a high density and a high canopy, and the plots with a low density and a low canopy. The observed architecture was heterogeneous, which is surprising since, in general, a high density corresponds to small diameters and low height. The identification of the species with the maximum height (six species) suggests that their ability to quickly cover the canopy would be bound to their temperament. These species have developed specific strategies with respect to light, to grow as fast as possible in reference to the concept of ecotop (Oldeman 1974). This mainly concerns *Aucoumea klaineana* Pierre, which was found as a dominant canopy species in four of the five structural groups, and also *Lophira alata* Banks ex Gaertn. and *Dacryodes buettneri* (Engl.) H.J.Lam. When considering the maximum height and the mean height, two structural sets in the sense of Oldeman (1990) can be clearly distinguished: two arborescent layers including the trees of the higher layer on the one hand, and emergent trees on the other hand. Similar results were found in Ivory Coast (Devineau 1975, 1984, 1991).

In terms of basal area, if we consider the total basal area as a proxy for the degree of cover, the result show a gradient (20–58 m² ha⁻¹) from recently disturbed plots (right hand



Figure 7 – Projection of species on the first two axes of the canonical correspondence analysis of the species abundances at Lopé, Gabon. The size of dots is proportional to the square root of species abundances.

side of the gradient) to undisturbed plots (left hand side). These values are found in secondary forest, thus indicating that the five structural groups are consistent with secondary forests (Bongers & Blokland 2004, Nyare 2004). In comparison with the results found in the Itchède forest in Benin (Awokou et al. 2009) and in the Una forest in north-eastern Brazil (Faria et al. 2009), the peaks of basal area were obtained for diameters between 35 and 55 cm. We can deduce from this that the structural groups also correspond to an evolution from young secondary forests to old secondary forests (Gazel 1983). In the Dja reserve, Sonké (2004) found values between 26 and 39 m² ha⁻¹ for the facies of typical heterogeneous forest, whereas in the Maya Biosphere Reserve, basal area varied between 40 and 66 m² ha⁻¹ depending on the level of disturbance of the plots (Nesheim et al. 2010). In this study, the value of 58 m² ha⁻¹ in basal area corresponded to floristic group 6 and structural group 5. This value was found for the so-called Maranthaceae forests in the Lopé National Park (White et al. 1995, Nasi 1997).

Floristic characteristics

A patchy distribution was observed for many species, which also appeared from the comparison of structural group for density, height and basal area. Plots and transects crossed different forest types as described by White (1996) regarding to abiotic factors such as water, rocks, altitude (White 2007). A gradient of forest types was observed (fig. 3): at one end were the floristic groups associated to the river Ogooué; the centre of the gradient corresponded to the colonizing forests and to the forests associated to rocks; and the right hand side of the gradient corresponded to the altitude forests as described by White (1996). This type of gradient was observed in the forests of the plains of South East Liberia and South West Ivory Coast by Van Rompaey & Oldeman (1996). On the basis of a CA, these authors also evidenced an ordination of the species and plots along a principal gradient.

Similarly to what was observed in Ghana (Hawthorne 1996), the gradient observed on the first axis of the CA (fig. 3) can be interpreted as a 'forest type gradient'. Sometimes this pattern means that the species that compose the forest have a large distribution, which could be investigated by studying their phytogeography. The observed forest recovery also expressed in the structural groups, from the groups with a high species richness in the canopy, a low density but many small individuals (groups 1 and 4), to the dense groups with many large individuals that corresponded to a floristic stability (groups 2 and 5). Between-transect as well as within-transect floristic differences were observed (fig. 5). Nearby plots often had opposite variations. The floristic variations that were evidenced were related to the variations of the forest structure (case of transects 2 and 4). Other studies have also indicated that the species composition may be a better indicator of the forest structure than just diversity (Onaindia et al. 2004 and references therein). This type of results was also obtained in West Indies (Rousteau 1996) when dealing with the variations of species composition and of the forest structure along an altitudinal gradient.

Relationship between structural and floristic characteristics

Although the observed gradient cannot be explained by structural variables alone, there was a significant relationship between floristic groups and structural groups. This relationship enabled us to distinguish structural groups on the basis of species abundances, with density (with the highest contribution from the small classes N_2 and N_3) and height being the best discriminating variables. The variations of canopy species diversity and of floristic composition in our study are similar to those obtained by Schulz (1960). Species are locally abundant and globally rare.

Our results suggest that the future development of the forest canopy would involve a slow invasion of the upper canopy by emergent species. Studies on the dynamics of forest formations in the Lopé National Park (White 1996) showed that there was a tendency to monodominant forest types, which is consistent with the typology of secondary forests in Gabon, in particular secondary forests with okoumes (Nyare 2004). The two most exploited tree species in Gabon, *Aucoumea klaineana* Pierre (okoume) and *Dacryodes buettneri* (Engl.) H.J.Lam (ozigo), were those with the greatest height in the identified structural groups. This confirms their light-demanding and secondary temperament, and also the strong expansion of okoume as already notified by White et al. (2000) and Born (2007). The characterization of the vegetation groups in the Lopé National Park confirmed that it was composed of secondary forest, and showed that recent disturbances were expressed by floristic associations of species with broad distributions (Hawthorne 1996). Hence, the forest under study at Lopé is a forest mosaic in progression. These results are in agreement with the concept of the silvatic mosaic by Oldeman (1990). Similar results were found in Poland (Bobiec et al. 2000).

The predominance of okoume in the five identified structural groups suggests a tendency to a monodominant climax, in agreement with the forest type described in the Lopé National Park by White (1996). The observed floristic gradient and species abundances can be explained by a local overabundance of light-demanding species. Light is the resource that explains the vertical structure of the forest, the species diversity within the canopy, and the variations of floristic composition across structural groups. Our results evidenced that the forest at Lopé was a dynamic system where forest was recovering, and that the current forest structure was the outcome of the interplay between the forest savanna mosaic on the one hand, and recent and current disturbances on the other hand. In a future work, species traits will be studied in relation with floristic groups at the Lopé National Park, and the evolution of the mosaic will be predicted under a conservatory management plan where fire is used as a tool to maintain the neighbouring savanna.

ACKNOWLEDGEMENTS

We thank the following people for their contribution in the field, Kathryn J. Jeffery and the technical team field of SEGC. We thank the Centre International de Recherches Médicales de Franceville (CIRMF/SEGC) for logistical support to this study, and UMR 7179 (Brunoy/MNHN) for financially

supporting our AETFAT conference participation. We thank WCS Gabon, the NERC-UK, the Leverhulme Trust, WOTRO-Netherlands and the Wellcome Trust for funding the data collection for this study.

SUPPLEMENTARY DATA

Supplementary data are available at Plant Ecology and Evolution, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consist of the following: (1) additional multivariate analyses of floristic and structural data (pdf format).

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Manuscript received 14 Jul. 2010; accepted in revised version 16 Feb. 2011. This paper was pre-published on 15 Nov. 2011 in issue 144(3) of *Plant Ecology and Evolution*.

Communicating Editors: Brice Sinsin & Elmar Robbrecht.



Endemism, species richness and morphological trends in Madagascan *Memecylon* (Melastomataceae)

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Background and aims – Further studies of Madagascan *Memecylon* have revealed that much of the herbarium material collected in the last 25 years is undescribed. As a prelude to a comprehensive taxonomic revision, the current paper presents an overview and analysis of the remarkable diversity of this genus in Madagascar.

Key results – Within the paleotropical distribution of *Memecylon*, Madagascar contains by far the highest concentration of species proportionate to land area. All of the Madagascan *Memecylon* species are endemic to the island, with the majority being localized endemics known from just one or two sites. As a result of recent field- and collections-based studies, about fifty new species will be proposed. When this is done the total number of Madagascan *Memecylon* species will increase to 138 (representing a 70% increase from our state of knowledge in 1985). *Memecylon* is clearly one of the plant genera that has radiated extensively on the island. Floral morphology is strongly conserved, but leaf morphology and inflorescence position are quite variable and often diagnostic at the species level. In several cases, different species have converged on similar vegetative morphologies, leading to taxonomic confusion.

Conclusions – When making species determinations in Madagascan *Memecylon*, both morphological features and ecogeographic factors should be taken into account. Comprehensive taxonomic revisions in species-rich groups like *Memecylon* are a prerequisite for further study of the mechanisms of species diversification on the island.

Key words – diversification, endemism, Madagascar, Melastomataceae, *Memecylon*, plant taxonomy.

INTRODUCTION

The paleotropical genus *Memecylon* L. consists of forest-understory trees and shrubs with very hard wood; opposite, stipulate, apparently uninervate leaves; small, 4-merous flowers; and berry-like, 1-seeded fruits. The flowers in this and other members of Melastomataceae, subfamily Olisbeoideae are peculiar in having enlarged anther connectives often bearing a conspicuous gland on the dorsal side (see fig. 1 in Stone et al. 2006). In the neotropical genus *Mouriri* Aubl., the secretion from these anther-glands is rich in fatty oils (Buchmann & Buchmann 1981). The flowers of *Memecylon* are thus presumably pollinated by oil-collecting bees, although this remains to be investigated.

The geographic distribution of *Memecylon* encompasses tropical Africa and Indo-Malesia, with added occurrences on islands of the Indian Ocean including Madagascar, Mayotte, the Mascarenes, and the Seychelles. The last comprehensive monograph of the genus was that of Cogniaux (1891), and since then more than 350 new species or varieties have been proposed by various authors. In addition, 45 species previ-

ously included in *Memecylon* have been transferred to the segregate genera *Spathandra* Guill. & Perr. (one species, West & Central Africa), *Lijndenia* Zoll. & Moritz (fifteen species, paleotropical), and *Warneckea* Gilg (fifty species, Afro-Madagascan) (Jacques-Félix 1978, Bremer 1982, Stone 2006a, Stone & Andreasen 2010). As currently circumscribed, *Memecylon* sensu stricto comprises more than 300 recognized species and infraspecific taxa (Renner et al. 2007 onwards).

With regard to *Memecylon* of Madagascar, the most recent treatment (Jacques-Félix 1985a, 1985b) recognized 78 species of which 34 (44%) were newly described. My own studies of Madagascan *Memecylon* began in 2001, while I was still a Ph.D. student at the University of California, Berkeley. At that time, duplicate specimens distributed by the Missouri Botanical Garden were already accumulating in the herbarium of the California Academy of Sciences (CAS). In 2002, I had the opportunity to study types and other collections in the Muséum d'Histoire naturelle, Paris (P). It soon became evident that much of the recently collected Mada-

gascan material represented species new to science (cf. Stone 2006b). From 2006 to 2008, I was fortunate to be the holder of a postdoctoral fellowship at CAS, which allowed me to continue my field- and collections-based research on *Memecylon*, the main objective being to complete a taxonomic revision of the Madagascan species.

As a precursor to the taxonomic revision of *Memecylon* in Madagascar, the current paper summarizes our knowledge of the patterns of endemism and species richness, as well as the morphological trends exhibited by the Madagascan members of this genus. Not reported here are the results of preliminary phylogenetic analyses based on sequences of the ETS and ITS regions of nuclear ribosomal DNA (R.D. Stone, unpubl. res.). These will be submitted for publication separately, following completion of a currently funded project to sequence an additional 81 samples of *Memecylon* from Madagascar and the Mascarene Islands.

MEMECYLON IS AMONG THE MOST SPECIES-RICH GENERA IN THE WOODY FLORA OF MADAGASCAR

When one apportions the species richness in *Memecylon* by geographic region, it is at first evident that the Asian tropics have the most species (fig. 1). However, this could be at least partially explained by the fact that the Asian tropics have a much larger area ($5,903 \times 10^3 \text{ km}^2$) in comparison to tropical Africa ($3,471 \times 10^3 \text{ km}^2$) or Madagascar ($112 \times 10^3 \text{ km}^2$).

The plot of *Memecylon* species richness versus area (fig. 1) contains six data points, not all of which are independent since the island of Borneo is really a subdivision of the Asian tropics. However, if one is willing to assume that the general species–area relationship is represented by a line fitted through the points for the Comoros, the Mascarenes, Borneo, and the Asian tropics, then the species numbers in tropical Africa and Madagascar are clearly ‘below the line’ and ‘above the line,’ respectively.

The relatively low concentration of *Memecylon* species in tropical Africa is consistent with the general impoverishment of the African forest flora – which led Richards (1973) to characterize Africa as the “odd man out” relative to the forests of the Asian and American tropics. On the other hand, the exceptionally high concentration of *Memecylon* species on Madagascar is in agreement with the generally high species richness and endemism seen in the flora of the island (Myers et al. 2000, Gautier & Goodman 2003, Phillipson et al. 2006). In comparison to Madagascar, the original extent of forest on Borneo is more than six times larger ($743 \times 10^3 \text{ km}^2$), yet the number of *Memecylon* species is evidently much lower.

Based on species numbers reported in the *Generic tree flora of Madagascar* (Schatz 2001), it is apparent that most of the nearly 500 woody genera on the island are represented by relatively few species (fig. 2). It is also evident that *Memecylon* is one of the genera that has radiated extensively in Madagascar (table 1).

Table 1 – The ten most species-rich genera in the woody flora of Madagascar.

Data from Schatz (2001).

Genus	Family	No. of Madagascan species
<i>Dombeya</i>	Malvaceae	180
<i>Croton</i>	Euphorbiaceae	150
<i>Euphorbia</i>	Euphorbiaceae	150
<i>Dyopsis</i>	Arecaceae	137
<i>Diospyros</i>	Ebenaceae	100
<i>Oncostemum</i>	Myrsinaceae	100
<i>Grewia</i>	Malvaceae	86
<i>Senecio</i>	Asteraceae	85
<i>Pandanus</i>	Pandanaceae	85
<i>Memecylon</i>	Melastomataceae	78

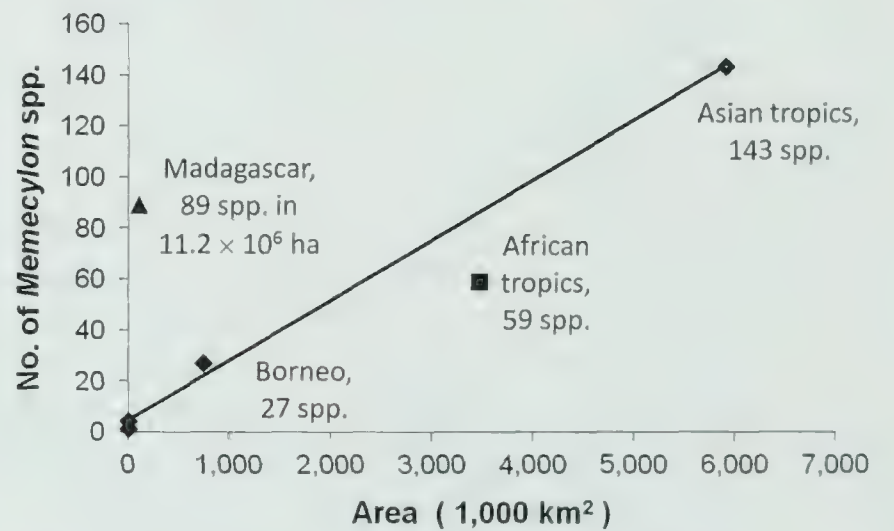


Figure 1 – Species–area relationships of the genus *Memecylon* by geographic region (the two unlabeled points near the origin are for the Comoro and Mascarene islands, respectively). The line is fitted to all points except Madagascar and the African tropics. Species numbers are from published sources (Bremer 1983, Jacques-Félix 1985a, 1985b, Wickens 1990, Stone 2006b, Renner et al. 2007 onwards). Estimated original extent of the Madagascan rain forest is from Green & Sussman (1990). Areas of the African and Asian tropics are from World Wildlife Fund (cited by Fine & Ree 2006). Total island area was used for Borneo, the Mascarenes, and the Comoros since no precise estimates of the original extent of forest could be found.



Figure 2 – Species richness amongst woody genera in the Madagascan flora (data from Schatz 2001).

HISTORY OF DISCOVERY

Du Petit-Thouars, Chapelier, and Goudot were the earliest scientific collectors of *Memecylon* in Madagascar. The first Madagascan species to be formally described was *M. ulopterum* DC. (1828). Subsequent authors contributing new *Memecylon* species included Blume, Naudin, Baker, Cogniaux, Richard Émile Augustin de Candolle, Danguy, Perrier de la Bâthie, Jacques-Félix, and R.D. Stone. Four major events in the history of knowledge of Madagascan *Memecylon* are here identified:

- 1 Naudin (1852) added nine new species.
- 2 Perrier de la Bâthie (1932) added 26 new species.
- 3 Jacques-Félix (1985a, 1985b) proposed 36 new *Memecylon* species, but in the same treatment three previously described species were relegated to synonymy, and eleven species originally described in *Memecylon* were transferred to *Lijndenia* or *Warneckea*. The overall effect was a net gain of 22 species.
- 4 Stone (2006b) contributed eight new species, and his subsequent field and herbarium studies have revealed an additional 50+ species (R.D. Stone, unpubl. res.). When these are formally published, it will raise the number of known Madagascan *Memecylon* species to at least 138 (representing a 70% increase from the state of knowledge in 1985).

This history of knowledge can be represented as a “species discovery curve,” i.e. a plot recording the cumulative number of species recorded in a given area over time (fig. 3). As the inventory of Madagascan *Memecylon* nears completion, one would expect this curve to level off as new species become more and more difficult to find. Thus far, however, the curve appears to be increasing in a roughly linear fashion, and there is no suggestion of a decline in the rate at which new species are being discovered. Hence using this approach, it is difficult to suggest what the final number of Madagascan *Memecylon* species might be. Bebbier et al. (2007) have recently criticized the method of estimating species richness from rates of species description, noting that the discovery rate depends not only on the number of spe-

cies remaining to be found, but also on the intensity of the discovery effort. Alternative approaches exist but are computationally intensive or prone to sampling error (cf. Beck & Kitching 2007).

The large number of recently discovered species of Madagascan *Memecylon* is remarkable but not extraordinary, as intensified field work over the past 25 years “has revealed high numbers of undescribed species in numerous Malagasy animal and plant groups, sometimes outnumbering those already described” (Vences et al. 2009). For example, a recent monograph on the palms of Madagascar (Dransfield & Beentje 1995) contained descriptions of eighty new species, representing a 46% increase in the known palm flora of the island. Hedge et al. (1998) described 58 new Madagascan species in the family Lamiaceae (a 70% increase in the total known diversity of this group), and, according to Fischer et al. (2007), the known Madagascan species of *Impatiens* (Balsaminaceae) have more than doubled in the last half-century (from 105 to 231 species including many yet to be described).

Another aspect of the history of knowledge is the number of years that have elapsed since a particular species was last collected. For Madagascan *Memecylon*, this sort of analysis seems to indicate that the majority of species have been collected at some time during the last two decades (fig. 4). However, a closer inspection of the data reveals that many of these recently collected species are local or regional endemics that had never been collected before. It is an unfortunate fact that several of the *Memecylon* species collected more than eighty years ago have not hence been seen:

Species	Year	Locality
<i>Memecylon alatum</i> Aug.DC.	1897	near Maroantsetra
<i>Memecylon dalleizettei</i> H.Perrier	1907	Ivoloina, near Tamatave
<i>Memecylon</i> <i>subcuneatum</i> H.Perrier	1912	near Mananara-Nord
<i>Memecylon</i> <i>mananjebense</i> H.Perrier	1913	Sambirano region
<i>Memecylon</i> <i>pseudomyrtiforme</i> H.Perrier	1914	near Soalala (Ambongo-Boina)
<i>Memecylon</i> <i>tsaratananense</i> (H.Perrier) Jacq.-Fél.	1923	Mont Tsaratanana
<i>Memecylon aberrans</i> H.Perrier	1925	Analamazaotra (near Andasibe)
<i>Memecylon humbertii</i> H.Perrier	1928	Mont Papanga (Beampingaratra)
<i>Memecylon subsessile</i> H.Perrier	1928	Ambatovola (Moramanga)

Given the large extent of anthropogenic deforestation in Madagascar, one has to consider the possibility that some of these so-called “forest phantoms” may have been localized endemics that are already extinct. Others may not be

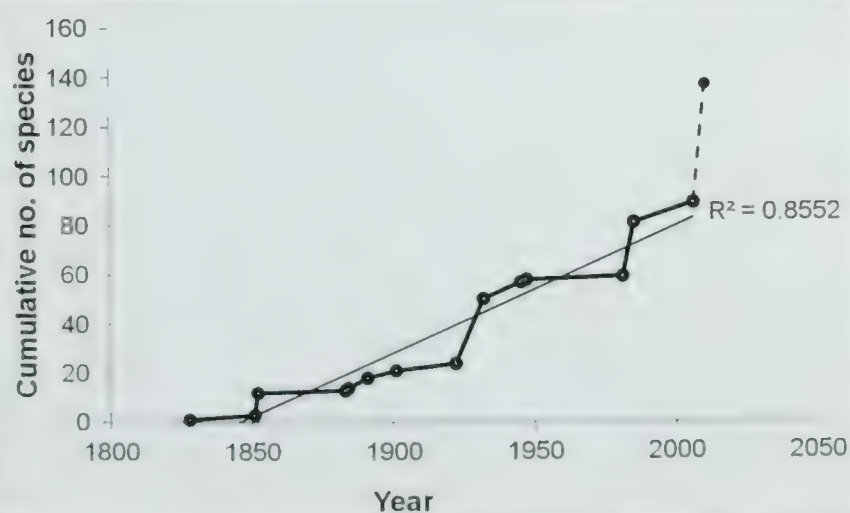


Figure 3 Species discovery curve for Madagascan *Memecylon*. The solid lines are based on dates of publication, while the dashed line represents newly identified species (R.D. Stone, unpubl. res.). See text for further details.

extinct, just very rare. For example, *M. crassinerve* Blume is endemic to Nosy Bé (an island off the coast of northwestern Madagascar). Of this species there were very few collections, the last one evidently by Hildebrandt in 1879. Happily, *M. crassinerve* (fig. 5) was recently rediscovered by my colleague Rokiman Letsara after a hiatus of more than 125 years. Success stories like this offer hope that, with additional field work, more of these “forest phantoms” may be found.

PATTERNS OF ENDEMISM

The non-random geographic distribution of *Memecylon* in Madagascar is especially apparent when one superimposes the distribution on a bioclimatic map of the island (fig. 6). Most of the species occur in the eastern rain forests or in the northwest to extreme north (Sambirano and Antsiranana regions). Relatively few *Memecylon* species are found on the central plateau or in the dry, largely deciduous forests of the western part of the island:

Central Plateau	Western Region
<i>Memecylon bakerianum</i> Cogn.	<i>Memecylon ankarensis</i> H.Perrier
<i>Memecylon centrale</i> (Jacq.-Fél.) R.D.Stone	<i>Memecylon boinense</i> H.Perrier
<i>Memecylon minimifolium</i> H.Perrier	<i>Memecylon buxifolium</i> Blume
<i>Memecylon vaccinioides</i> H.Perrier	<i>Memecylon</i> <i>pseudomyrtiforme</i> H.Perrier

Also notable is the virtual absence of *Memecylon* from the southern and southwestern region of Madagascar, where the climate is subarid and forested habitats are of extremely limited extent.

In the previous revision of Jacques-Félix (1985a), the *Memecylon* species of Madagascar were all regarded as endemics, with the exception of *M. mocquersii* Aug.DC.

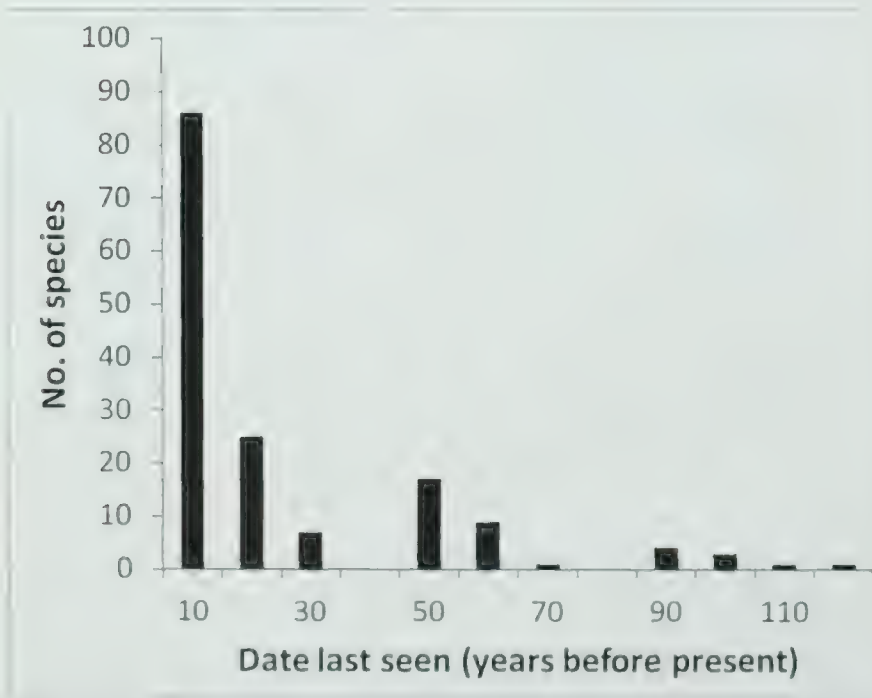


Figure 4 – Frequency distribution of the date last collected amongst Madagascan *Memecylon* species.

which was treated as conspecific with the Tanzanian species *M. cogniauxii* Gilg. Since that time, however, additional herbarium material has become available for study, and at least eight morphological characters have been found that reliably separate these taxa; the two lineages also differ at the DNA sequence level (uncorrected ETS divergence = 5.0%, ITS1 + ITS2 divergence = 4.8%) with preliminary phylogenetic analyses placing them in separate species-groups (R.D. Stone, unpubl. res.). From these new results it is clear that the resemblance between *M. mocquersii* and *M. cogniauxii* is only superficial. With *M. mocquersii* re-established as a separate species, the Madagascan *Memecylon* species are now considered to be 100% endemic. This agrees with analyses across multiple plant groups indicating that greater than 90% of Madagascan plant species occur nowhere else (Philipson et al. 2006). Amongst the trees and large shrubs, the level of endemism is even higher, approaching 96% (Schatz 2000).

Analysis of the number of known occurrences of Madagascan *Memecylon* species (fig. 7) indicates that 106 species are found in just one or two sites, suggesting that they are localized endemics. On the other hand, only four species are known from more than fifteen sites: *M. bakerianum* Cogn., *M. buxifolium* Blume, *M. louvelianum* H.Perrier, and *M. eduliforme* Aug.DC. The predominance of local endemism amongst the *Memecylon* species of Madagascar fits a general pattern of microendemism and high spatial species turnover seen in many of the plant and animal groups that have radiated on the island (Vences et al. 2009).

MORPHOLOGICAL DIVERSITY AND CONVERGENCE

Not only is Madagascan *Memecylon* amazingly rich in species; it also exhibits a range of morphological variation that is at least as wide as that seen throughout the rest of the widespread paleotropical distribution of the genus. The leaves, for example, range from very small, even microphyllous in certain species to very large in others (electronic appendix 1). The position of the inflorescence is also quite variable; depending on the species it may be borne terminally on the branchlets; in the axils of the leaves; at the thickened, leafless nodes of older branchlets; or even in dense patches down the trunk.

In addition to this wide morphological variation, evolutionary convergence on similar vegetative morphologies has led to species being misidentified, or in some cases to new species not being recognized when they should have been. Here I will present just one of several examples of morphological convergence amongst Madagascan *Memecylon*. In electronic appendix 2A, one sees an image of the holotype of *M. infuscatum* Jacq.-Fél., a species having a rather wide distribution in the littoral forests of eastern Madagascar. The type of *M. infuscatum* was collected in the Station Forestière de Tampolo (Toamasina province), and in electronic appendix 2B is shown an image of a second specimen (SF 16639) collected from the same locality and having leaves closely resembling those of *M. infuscatum*. On the basis of this second specimen, the fruits of *M. infuscatum* were originally described as being 20 mm in diameter (Jacques-Félix 1985b), but subsequent collections have revealed that the authentic



Figure 5 – *Memecylon crassinerve*, an endemic of Nosy Bé that was rediscovered in March 2008 after a hiatus of more than 125 years. A, leaves; B, flowers (photographs by R. Letsara).

M. infuscatum has fruits that are much smaller (c. 5 mm in diameter). With the discovery of additional flowering material in the TEF herbarium, the vegetative resemblance be-

tween *M. infuscatum* and the large-fruited species is shown to be superficial (see electronic appendix 3 for a comparison of the flowers of *M. infuscatum* with those a second, as-yet undescribed species from SF Tampolo). The real affinities of the large-fruited species appear to be with the group that includes *M. eglandulosum* H.Perrier, *M. bezavonense* (Jacq.-Fél.) R.D.Stone, *M. planifolium* Jacq.-Fél., *M. tsaratananense* (H.Perrier) Jacq.-Fél., and *M. antseranense* Jacq.-Fél.

CONCLUSIONS

The combination of high species richness, rampant micro-endemism, and morphological convergence in Madagascan *Memecylon* indicates the importance of taking ecogeographic factors into account when making species identifications in this group. In other words, good species identifications are not simply a matter of rapid pattern-matching in the herbarium. If a new sample is not from the same forest, or at least from the same region as previous collections, then one has to consider the possibility that it belongs to a different species.

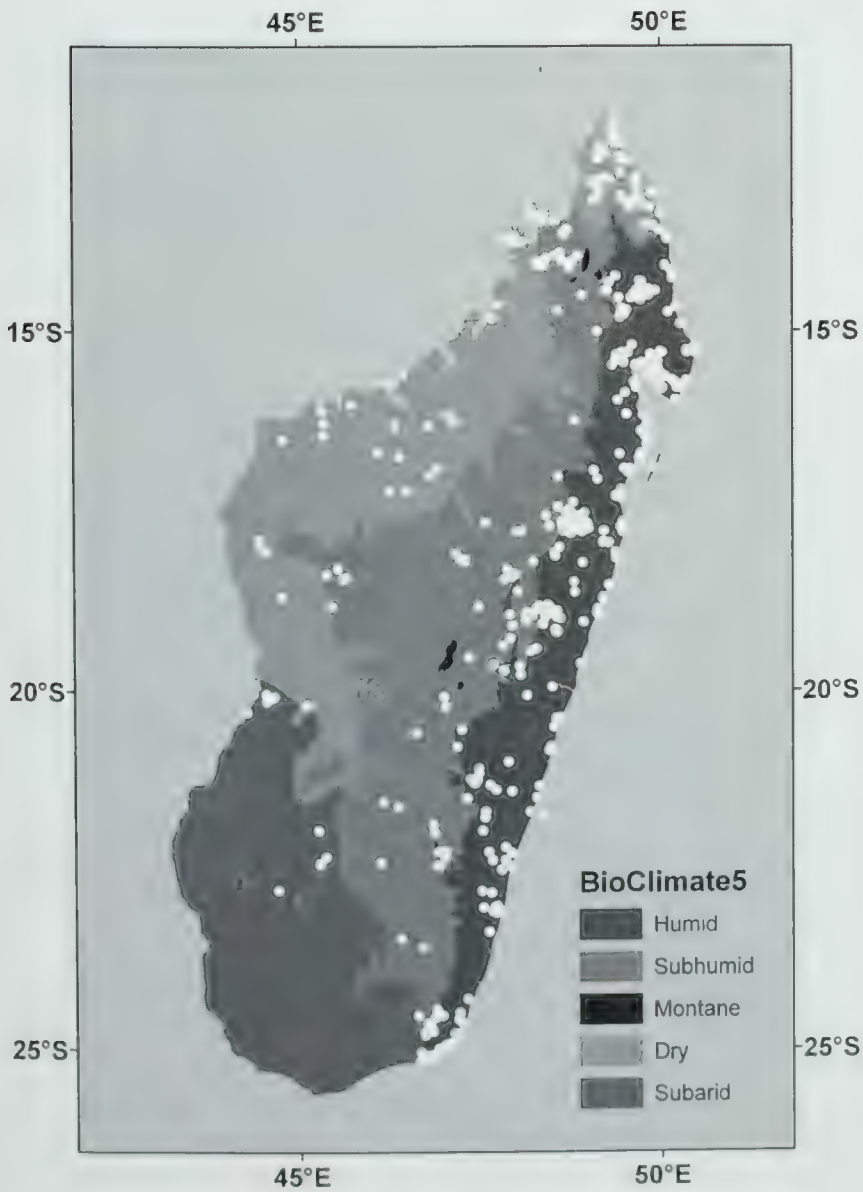


Figure 6 – Geographic distribution of Madagascan *Memecylon* (all known collections), superimposed on the 5-zone bioclimatic map of Cornet (1974).

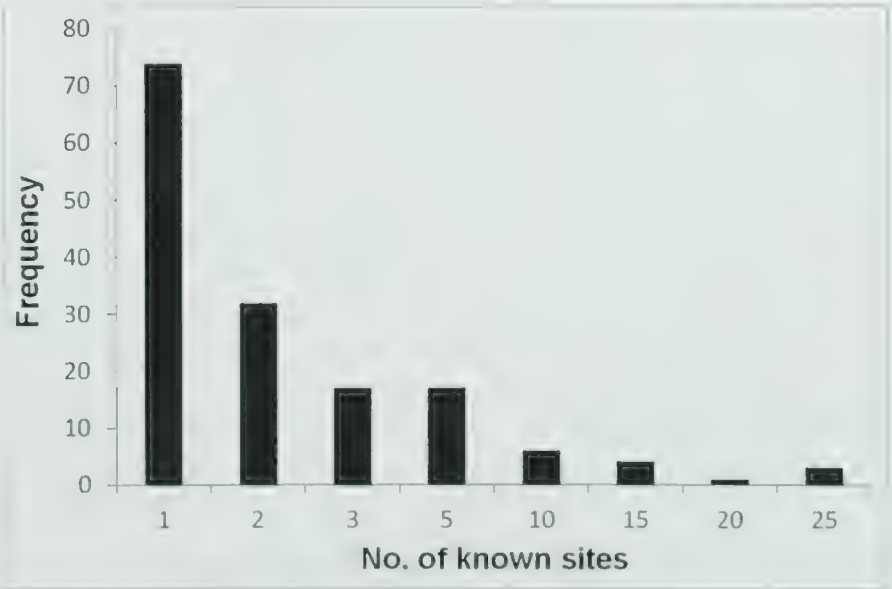


Figure 7 – Frequency distribution of the number of known sites amongst Madagascan *Memecylon* species.

This conclusion echoes a previous observation by Phillipson et al. (2006), that “most species in Madagascar have distribution patterns that are strongly correlated with reasonably well understood eco-geographic parameters.”

Madagascar’s long period of isolation from Africa and other land masses presents a unique opportunity to study endemic radiations of tropical biota (Vences et al. 2009). The mechanisms of diversification that have caused the prevalent pattern of microendemism on the island are currently an active area of research (e.g. Wilmé et al. 2006, Wollenberg et al. 2008, Pearson & Raxworthy 2009, Townsend et al. 2009). Thus far, however, most of the studies on speciation mechanisms have focused on animal groups, and there have been relatively few such studies involving plants (Vences et al. 2009, and references therein). Plant groups like *Memecylon* that have radiated extensively in Madagascar could nevertheless prove to be important model systems for further investigation of the mechanisms of species diversification. However, as noted by Vences et al. (2009), dense taxonomic sampling is necessary for studies of diversification, and comprehensive taxonomic revisions are therefore a prerequisite. More generally, as long as a substantial proportion of Madagascar’s plant diversity remains undescribed, this lack of knowledge is a “taxonomic impediment” (sensu Hoagland 1996) that hinders not only our progress in understanding the origin of species, but also their ecology and conservation.

SUPPLEMENTARY DATA

Supplementary data are available in pdf format at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consists of the following: (1) range of variation in leaf size amongst Madagascan species of *Memecylon*; (2) convergence in vegetative morphology in two *Memecylon* species from the Station Forestière Tampolo (Toamasina province); (3) comparison of floral morphology in two *Memecylon* species from the Station Forestière Tampolo.

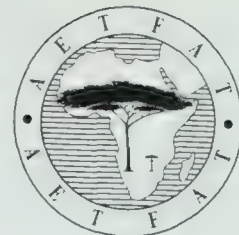
ACKNOWLEDGMENTS

Support for this research was provided by the Department of Integrative Biology, University of California, Berkeley, and the California Academy of Sciences (John J. Rose Post-doctoral Fellowship). Field work in Madagascar was done in cooperation with the Association Nationale pour la Gestion des Aires Protégées, Fanamby, the Madagascar Institute for the Conservation of Tropical Environments, the Missouri Botanical Garden, and the Water & Forestry Department, University of Antananarivo. The curators of the following herbaria are thanked for facilitating access to specimens or loans thereof: BR, CAS, G, K, MO, NU, P, TAN, TEF, UPS. The manuscript has been improved by comments from two anonymous reviewers.

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- Manuscript received 30 Sep. 2010; accepted in revised version 13 Feb. 2012. This paper was pre-published on 6 Jul. 2012 in issue 145(2) of *Plant Ecology and Evolution*.
- Communicating Editor: Thomas Haevermans.



The history of palm exploration in Madagascar

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Context – Palms are among the most diverse families of plants in Madagascar but knowledge of the family remains incomplete. Compared with other plants, only few botanists have actively worked on the family.

Aim – This paper aims to relate palm research in Madagascar chronologically since the 18th century by highlighting the evolution of knowledge of palm taxonomy over time.

History – Since 1770, when Philibert Commerson collected the first palm samples in Madagascar, approximately 2100 herbarium specimens have been made by 163 researchers, stored in herbaria across the world. The history of palm exploration on the island is rich and palm knowledge has been marked by frequent changes in taxonomic delimitation. Many palms have been renamed several times as different species or even in different genera. From 1950, H. Humbert, J.L. Guillaumet and then H.E. Moore made efforts to resolve palm taxonomic problems in Madagascar. Resolution was achieved only with the publication in 1995 of *The Palms of Madagascar*, by John Dransfield and Henk Beentje, which has led on to many subsequent discoveries.

Key words – History, palm exploration, taxonomy, Madagascar.

INTRODUCTION

Following the discovery of the island of Madagascar by the Portuguese explorer Diego Dias in the early 1500s, European naturalists began to be interested in the exploration of the resources of Madagascar. Foremost among the naturalists was Etienne de Flacourt who arrived in Madagascar in 1648 and contributed much to the promotion of the fauna and flora of the island, especially in Fort-Dauphin region, until his departure in 1655. In his *Histoire de la Grande Isle de Madagascar*, de Flacourt (1658, reprinted 1991) celebrated the great number of rare plants as well as animals on the island. The first impression of the early naturalists was the fact that the fauna and the flora are peculiar and characterized by high endemism compared with other tropical areas that had already been studied at that time. However, the first important floristic exploration occurred only at the end of 18th century when Philibert Commerson visited the island in 1770 and 1771. Commerson collected 495 plant species during this trip, among them the first collections of palms ever made from the island.

Palms are very diverse and display a high rate of endemism in Madagascar. The latest census reports the occurrence of seventeen genera and 195 native species; all but five of these species are endemic to the island (Dransfield & Beentje 1995a). In addition, the species diversity is estimated to be three times larger than in the continent of Africa

(Govaerts & Dransfield 2005). Distributions of palms across the island are not, however, uniform. More than 90% of the currently known species inhabit the eastern region (Rakotoarinivo 2008). Although palms are important components of the humid primary vegetation in Madagascar, only few botanists have actively studied the family (Dransfield & Beentje 1995a). Frequently large dimensions and bulkiness of the plants present challenges to making specimens and this explains the paucity and fragmentary nature of specimens stored in herbaria. Although palm research has been less intensive compared to some other groups of plants, the history of palm exploration in Madagascar is characterized by frequent changes in taxonomy and nomenclature. This paper aims to relate palm research in Madagascar chronologically since the 18th century by highlighting work done by researchers up until today, taxonomic changes through the ages and finally the geography of studied areas and their impact on the knowledge of palms in Madagascar.

PALM RESEARCH SINCE THE 18TH CENTURY

Since the first collection of palms made by Philibert Commerson in 1770–1771 in Fort-Dauphin and the region of the Bay of Antongil, about 2100 different samples of palms have been collected in Madagascar based on specimens currently stored in different herbaria around the world. As plant researchers in Madagascar were mostly from France between

the 18th and the first half of the 20th century, most of the old specimens are housed in the Paris Herbarium (P). However, the herbaria of Kew (K), Antananarivo (Tsimbazaza, TAN) as well as Missouri (MO) own important numbers of palm samples in addition to those of Paris. Specimens of palms from Madagascar are also stored in a few other herbaria including New York (NY), Florence (FI), Bailey Hortorium (BH), Geneva (G) and Antananarivo (TEF).

Palm collectors and herbarium specimens

Up until today, 163 researchers are recorded as having collected palms in Madagascar. Most of these collectors, however, only occasionally collected palms, having made fewer than ten collections respectively. Not surprisingly, researchers of the last decades have collected more samples than naturalists before the 20th century (electronic appendix 1) since the ability to travel became easier and some researchers have specialized in palms. The two top collectors of palms in Madagascar, John Dransfield and Henk Beentje, made together nearly 800 samples, during the preparation of *The Palms of Madagascar* (Dransfield & Beentje 1995a). In addition, nearly $\frac{3}{4}$ of the currently known specimens have been collected during the last three decades, implying substantial progress in palm exploration and taxonomic knowledge during that period. However, it should be noted that earlier researchers have played a significant role in the history of palm exploration on the island. Among the researchers (electronic appendix 2) having worked on palms in the 19th century are Rev. Richard Baron (32 collections of palms) and in the first part of 20th century Henri Perrier de la Bâthie (183 samples), Henri Humbert (75 samples), Raymond Decary (34 samples), Gilbert Cours-Darne (33 samples) and also in the second part of 20th century, Jean-Louis Guillaumet (33 samples).

Almost all palm herbarium specimens collected before 1980 lacked geographic coordinates or even clear locations on their labels. The major problem for naturalists in the 20th century or earlier was the lack of good maps or exact locations of their study sites. Consequently, localities cited with plant specimens are generally incomplete or vague to the point that correct georeferencing remains difficult or impossible. For instance, one collection of Thiry in 1904 stated “from Eastern forest” and several collections of Rev. Baron have the origin “Central Madagascar”. Although it is known that Baron worked in Ambohidratrimo, Vonizongo, Manjakandriana, Antananarivo and Fianarantsoa (Dorr 1987) during his 25 years in Madagascar (1880–1905), determination of the origin of some specimens remains difficult as all of these localities are from the centre of Madagascar.

Areas surveyed for palms present gradual change and progress through time (electronic appendix 3). Given the high frequency of palms in the rainforest, the eastern region has been more intensively explored for palms when compared with the rest of Madagascar. About 97% of the currently known samples of palms in fact originate from the eastern region.

Before 1900 (electronic appendix 3a), areas surveyed for palms were mostly areas in the vicinity of Antananarivo (Moramanga, Manjakandriana and Ankazobe) or Fianarantsoa, but also from the Bay of Antongil, Sambirano area or

Fort-Dauphin. The main botanists of that period were Louis-Hyacinthe Boivin (collecting in Madagascar 1846–1852), Auguste Pervillé (1840–1841), Alphonse Charles Joseph Bernier (1822–1848) and Rev. Richard Baron (1880–1905).

The arrival of several scientists in the first half of the 20th century resulted in the exploration of new sites (electronic appendix 3b). Between 1896 and 1933, H. Perrier de la Bâthie and Henri Lucien Jumelle travelled mostly together throughout Madagascar but their main palm collections are from Andasibe, Betampona, Maroantsetra and Masoala Peninsula, Mangoro, Andringitra and Isalo. From 1910 to 1960, H. Humbert (sometimes associated with Gilbert Cours-Darne from 1936) explored mainly the highlands and collected palms for the first time from Marojejy, Mangindrano, Zahamena, and Andohahela mountains. The palms of the southern part of Madagascar (Amboasary Atsimo, Fort-Dauphin and Vondrozo) were explored by Raymond Decary between 1928 and 1942 (Decary in Madagascar 1916–1944).

Between 1950 and 1980 (electronic appendix 3c), palm research was carried out mostly by J.L. Guillaumet (1968–1973) and Harold E. Moore (1971–1972). Guillaumet travelled in several places in the eastern part of Madagascar and made additional collections, mostly, from Marojejy and Fort-Dauphin region. Moore devoted his trips to Andasibe, Masoala and Nosy Be with the expressed aim of obtaining material of poorly known endemic genera.

A substantial number of Madagascar palms specimens were collected between 1980 and 2000 (electronic appendix 3d), notably by John Dransfield (since 1986) and Henk Beentje (since 1991) who travelled in several parts of Madagascar. Dransfield and Beentje revisited areas previously explored by researchers but also worked in areas where palm collections had never been made. Fieldwork was located mainly in Marojejy, Manongarivo, Nosy Be, Masoala, Mananara Avaratra, Soanierana Ivongo, Betampona, Farafangana, Ankazobe, Tsiroanomandidy, Andohahela and the Fort-Dauphin area. Despite these intensive efforts, new areas have continued to be explored since 2000 (electronic appendix 3e). New researchers [William J. Baker (collections since 1998), Adam Britt (since 2001), Jeremie Razafitsalama (since 2002) and Mijoro Rakotoarinivo (since 2005)] interested in palm botany in Madagascar carried out their research in collaboration with Dransfield and Beentje. Consequently, new and often remote areas were investigated for the first time, such as Daraina, Galoka chain, Makira, Zahamena, Mangerivola, Vondrozo and the Vohimena chain in Fort-Dauphin. The years post-2000 are also marked by the expansion of general plant collecting across the island and palms benefited from different expeditions even if the samples from each locality do not always reflect the complete palm flora.

Naming palms

The first description of palms native to Madagascar was made by Carl von Martius in 1838 for two slender palms, *Dypsis forficifolia* and *D. hirtula*, collected respectively in the Bay of Antongil region. Today, seventeen genera and 195 species of Madagascar palms are accepted as legitimately published. Table 1 summarizes the current accepted genera, their synonym(s) and the number of their species.

Table 1 – List of accepted genera of Madagascar Palms.

Subfamily	Tribe	Accepted genus	Authorship	Year of publication	Synonym(s)	Number of species in Madagascar
Calamoideae	Raphiinae	<i>Raphia</i>	P.Beauv.	1806		1 (not endemic)
	Phoenixaceae	<i>Phoenix</i>	L.	1753		2 (not endemic)
	Chuniophoeniceae	<i>Tahina</i>	J.Dransf. & Rakotoarin.	2008		1 (endemic)
Coryphoideae	Borasseae	<i>Bismarckia</i>	Hildebr. & H.Wendl.	1881		1 (endemic)
		<i>Satranala</i>	J.Dransf. & Beentje	1995		1 (endemic)
		<i>Hyphaene</i>	Gaertn.	1790		1 (not Endemic)
		<i>Borassus</i>	L.	1753		2 (1 endemic, 1 not endemic)
Ceroxyloideae	Ceroxyleae	<i>Ravenea</i>	H.Wendl.	1878	<i>Ranevea</i> , <i>Louvelia</i>	19 (all endemics)
	Oranieae	<i>Orania</i>	Zipp.	1829	<i>Sindroa</i> , <i>Halmoorea</i>	3 (all endemics)
	Cocoseae	<i>Beccariophoenix</i>	Jum. & H.Perrier	1915		2 (all endemic)
		<i>Voanioala</i>	J.Dransf.	1989		1 (endemic)
		<i>Cocos</i>	L.	1753		1 (not endemic)
	Elaeidinae	<i>Elaeis</i>	Jacq.	1763		1 (not endemic)
Arecoideae	Dypsidinae	<i>Dypsis</i>	Mart.	1838	<i>Adelodypsis</i> , <i>Antongilia</i> , <i>Chrysalidocarpus</i> , <i>Dypsidium</i> , <i>Haplodypsis</i> , <i>Haplophloga</i> , <i>Macrophloga</i> , <i>Neodypsis</i> , <i>Phloga</i> , <i>Phlogella</i> , <i>Trichodypsis</i> , <i>Vonitra</i>	154 (all endemics)
		<i>Lemuropoenix</i>	J.Dransf.	1991		1 (endemic)
		<i>Marojejya</i>	Humbert	1955		2 (all endemics)
		<i>Masoala</i>	Jum.			2 (all endemics)

The rate of naming palms in Madagascar has increased progressively since 1838 but the description of new taxa has been made at different rates (fig. 1). High numbers of newly described species coincide mostly with periods where a particular naturalist has investigated in Madagascar. Of course, almost every specimen collected in the 19th and in the beginning of 20th century represented a new taxon as exploration had just begun. The number of species described remained surprisingly low until 1900 because few collections were made. The arrival of Perrier de la Bâthie in Madagascar in early 1900 increased the rate of collecting and naming palms. Between 1906 and 1912, Perrier collected 81 palms specimens (more than all the specimens that had been collected before). This resulted in the description of twenty new species and three new genera. Similarly with about 800 specimens collected between 1984 and 1995, Dransfield and Beentje described 78 new species from four different genera. Conversely, rather few specimens were collected during intervening years but the number of described species in-

creased. This is a result of the fact that some specimens collected earlier remained unidentified and new study resulted in their being named.

Palm botany in Madagascar has also been characterized by confusion in naming and species delimitation. Researchers had difficulty in the application of the species concept as many palms present strong morphological variability at the same location or from different geographical regions. For instance, in the Bay of Antongil region, the species *Dypsis forficifolia* is represented by two forms based on leaf shape, one with entire bifid leaves and the other with broad pinnate leaves. The holotype of this species has a relatively long petiole; hence palms having short petioles but similar habit were named differently: *Dypsis hirtula*, *D. littoralis* and *D. masoalensis*. Such confusion happened also in many species and resulted in the publication of 33 genera and 302 palm species names in Madagascar. In order to account fully for the history of taxonomic changes in palms in Madagascar, we shall focus our analysis on each genus currently accepted:

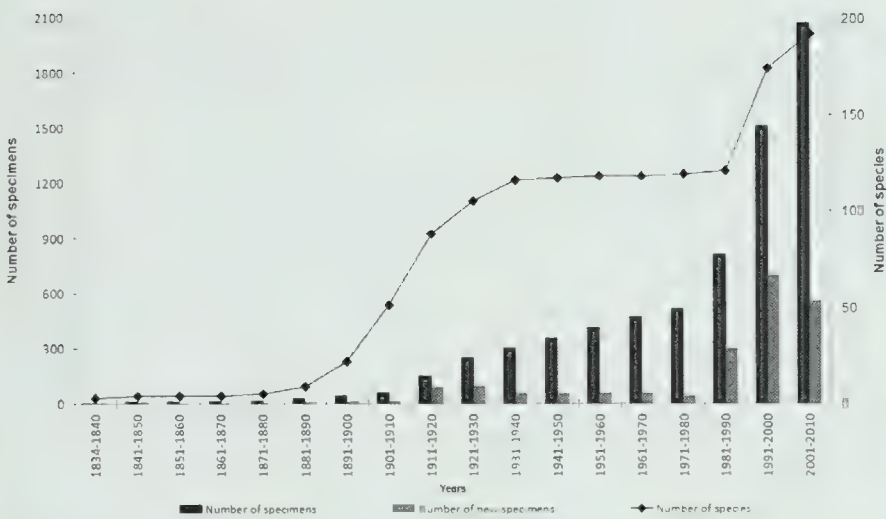


Figure 1 – Evolution of palms knowledge per decade. Black bars illustrate the total of palm specimens collected over time while grey bars refer to the number of specimens collected during the decade.

Table 2 – Chronogram of major change in the history of the genus *Dypsis* and its synonymized genera.

Year	Change in taxonomy
1838	Martius described the genus <i>Dypsis</i> (type species: <i>Dypsis forficifolia</i> Mart.)
1878	Wendland described the genus <i>Chrysalidocarpus</i> (type species: <i>Chrysalidocarpus lutescens</i> H.Wendl.)
1883	The genus <i>Phloga</i> was described (type species: <i>Phloga Nodifera</i> (Mart.) Noronha ex Salomon
1894	Baillon created 7 genera: <i>Neodypsis</i> (type species: <i>N. lastelliana</i> Baill.) <i>Neophloga</i> (type species: <i>N. commersoniana</i> Baill.) <i>Haplodypsis</i> (type species: <i>H. pervillei</i> Baill.) <i>Haplophloga</i> (type species: <i>H. poivreana</i> Baill.) <i>Dypsidium</i> (type species: <i>D. catatianum</i> Baill.) <i>Phlogella</i> (type species: <i>P. humblotiana</i> Baill.) <i>Trichodypsis</i> (type species: <i>T. hildebrandtii</i> Baill.)
1906	Beccari created two genera: <i>Vonitra</i> (type species: <i>V. fibrosa</i> (C.H.Wright) Becc.) and <i>Adelodypsis</i> (type species: <i>A. gracilis</i> (Bory) Becc.) in order to make a taxonomic framework for his Madagascar palm revision.
1914	Beccari established the genus <i>Macrophloga</i> (type species: <i>M. decipiens</i> (Becc.) Becc.)
1928	Jumelle described <i>Antongilia</i> (type species: <i>A. perrieri</i> Jum.)
1945	Jumelle and Perrier de la Bâthie made combinations in their palm revision: the genera <i>Trichodypsis</i> and <i>Adelodypsis</i> into <i>Dypsis</i> . the genera <i>Haplophloga</i> , <i>Dypsidium</i> and <i>Haplodypsis</i> into <i>Neophloga</i> . the genera <i>Phlogella</i> and <i>Macrophloga</i> into <i>Chrysalidocarpus</i>
1995	Dransfield and Beentje combined into <i>Dypsis</i> all the following genera: <i>Antongilia</i> , <i>Chrysalidocarpus</i> , <i>Neodypsis</i> , <i>Neophloga</i> , <i>Phloga</i> , and <i>Vonitra</i> .

Beccariophoenix –This genus was discovered in 1911 in Andasibe by Perrier de la Bâthie. The palm was named after O. Beccari, an Italian naturalist who worked on the taxonomy of Madagascar palms without having been on the island (Dransfield & Beentje 1995a). The type species is *B. madagascariensis*. This species had been thought to have disappeared from the wild since 1947, the last time Humbert recorded it in Fort-Dauphin. In fact, *B. madagascariensis* remained unseen in the wild until 1986 when Dransfield (1988) recorded the species at Mantady. The genus was thought also to be monotypic but a second species, *B. alfredii* (named after palm nurseryman Alfred Razafindratsira), was described from the western part of the Highlands of Madagascar (Rakotoarinivo et al. 2007). A third species is due to be described once adequate herbarium specimens are available.

Bismarckia – The genus was described in 1881 by J.M. Hildebrandt and H. Wendland to honor the German prince Otto von Bismarck-Schönhausen (Dransfield et al. 2008a). Only a single species, *B. nobilis*, is recorded in Madagascar. The genus *Bismarckia* is endemic to Madagascar but in 1904, R. Gallerand sank it into *Medemia*, a genus from Egypt to Sudan (Govaerts & Dransfield 2005), with the species name becoming thus *Medemia nobilis*. Very few botanists followed this taxonomic and nomenclatural change, and there are abundant reasons for maintaining *Bismarckia* as a distinct endemic genus (see Dransfield & Beentje 1995b and Dransfield et al. 2008a).

Borassus – The genus is not endemic to Madagascar as it also occurs in Africa, India, Southeast Asia and Malesia (Dransfield et al. 2008a). Among the two species in Madagascar, *B. madagascariensis* is endemic to the island while *B. aethiopum* is found also in mainland Africa (Govaerts & Dransfield 2005). Before, the name *B. sambiranensis* was utilized in Madagascar and considered as endemic (Jumelle & Perrier de la Bâthie 1945) but comparison with *Borassus* from Africa showed that it is not distinct from *B. aethiopum* (Bayton et al. 2003).

Cocos – The species *Cocos nucifera* is widely planted in the lowlands of Madagascar. It may represent one of the first crop plants to have been introduced to the island by the early immigrants from Indomalaysia (Dransfield & Beentje 1995a).

Dypsis – This genus, described in 1838 by C. Martius, has a long history given the previous confusion between it and 13 other genera that are all now regarded as synonyms (as shown in tables 1 and 2). *Dypsis* constitutes a complex and highly variable genus with species ranging from giant trees to dwarf or climbing palms (Dransfield et al. 2008a). As discussed in *Palms of Madagascar*, the taxonomic revision arose from the fact that the description of new species was frequently based on incomplete material in the past so researchers were forced to establish new generic names or revise them only a few years later. Hence, the distinction between these several genera remained for a long time ambiguous and superficial. For instance, the distinction between *Chrysalidocarpus* and *Neophloga* was based on the size of the palm and the number of pinnae (Palms large with many pinnae: *Chrysalidocarpus* / Palms small with few pinnae: *Neophloga*) while the type species of each of these genera

were of almost exactly the same size, with roughly the same number of pinnae (Dransfield & Beentje 1995a). Another example is *Dypsis heterophylla* which had been renamed eight times and placed into three genera from 1887 to 1929 (1887: *Dypsis heterophylla* and *Dypsis rhodotricha*, 1894: *Dypsidium emirnense* and *Dypsidium villersianum*, 1906: *Neophloga rhodotricha*, *N. emirnensis* and *N. majorana*, 1929: *Neophloga linearis* var. *distachya*). Such a situation happened in almost all described species before 1995. The taxonomic revision of *Dypsis* (Dransfield & Beentje 1995a) resulted in only 55 of these older species names being accepted as good species while the 125 other names known at the time were considered as synonyms. Dransfield & Beentje also described numerous new species in the genus. Today, the genus *Dypsis* includes palms having three or six stamens and with fruit having basal stigmatic remains (Dransfield & Beentje 1995a, Dransfield et al. 2008a). The genus is nearly endemic to Madagascar and constitutes about $\frac{3}{4}$ of the palm flora of the island. Of the 165 currently known species (Rakotoarinivo & Dransfield 2010), only two of them are in Comoros and one in Pemba, Tanzania (Dransfield & Beentje 1995a).

Elaeis – The genus is represented in Madagascar by a single possibly introduced species: *Elaeis guineensis*. The status of this species as native has been discussed by Beccari (1912) who distinguished a separate species (*E. madagascariensis*), followed by Jumelle & Perrier de la Bâthie (1913) who regarded it as a variety (*E. guineensis* var. *madagascariensis*).

Hyphaene – A genus of eight species present in Africa, Arabia, India and Sri Lanka. There is only one non endemic species in Madagascar: *Hyphaene coriacea*. Before 1995, the species name used in Madagascar was *H. shatan* but that is now synonymized in *H. coriacea*.

Lemurophoenix – Discovered by D. Halleux, J. Gerard and M.E. Darian, amateur palm enthusiasts, in the 1980s and described later by J. Dransfield (1991). *Lemurophoenix* is an endemic monotypic genus with the single species: *L. halleuxii*. However, seeds present in horticulture suggest that there may be a second undescribed species in the wild (Dransfield et al. 2008a).

Marojejya – A genus discovered and described by Humbert (1955) from his first exploration of the Marojejy massif. The genus comprises two species. The type species *M. insignis* remained poorly known until 1971 but today it has been shown to be among the most widespread species of the eastern rainforest. The second species, *M. darianii*, was discovered in the Maroantsetra region in 1983 by D. Halleux, J. Gerard and M.E. Darian and described only from fragments and photographs (Dransfield & Uhl 1984). Today, *M. darianii* is known to occur in a few sites in the northeast, between Brickaville and Maroantsetra.

Masoala – A genus of two species inhabiting rainforest. The type species, *M. madagascariensis*, was discovered by H. Perrier de la Bâthie in 1912 during his trip in Masoala Peninsula but described only two decades later by Jumelle (1933). This delay is due to the fact that Perrier's specimens gave little indication of its appearance and relationships (Dransfield & Beentje 1995a). The species was not collected again until 1986. Although its distribution range extends now between Marojejy and Toamasina area, *M. madagascariensis* remains

a rare palm. The second species, *M. kona*, was discovered by H. Beentje in 1991 in Ifanadiana area (Dransfield & Beentje 1995a). *M. kona* is endemic to the southeast, between Ifanadiana and Vondrozo area.

Orania – A genus with disjunct distribution range, in the Malesian region and Madagascar (Dransfield et al. 2008a). Three endemic species are present in Madagascar. The use of the genus name as *Orania* in Madagascar dates only from Uhl & Dransfield (1987) when the genus *Sindroa* (Jumelle 1933) was included in *Orania*. Another genus they described (*Halmoorea*) was later shown by Dransfield & Beentje not to be distinct from *Orania*.

Phoenix – This widespread genus, distribution range extending from Africa to Malesia (Dransfield et al. 2008a), is represented in Madagascar by two non endemic species. The date palm (*P. dactylifera*) is thought to have been introduced while the species *P. reclinata* is indigenous. Beccari (1906) considered even a variety for Madagascar (*P. reclinata* var. *madagascariensis*) but this infraspecific rank was abandoned by Dransfield & Beentje (1995a) during their taxonomic revision.

Raphia – This palm had been thought for a long time to be native in Madagascar with an endemic species *R. ruffia* (Martius 1823–1850); then R. Sabebeck proposed in 1904 the name *R. tamatavensis*. However, this last name was put in synonymy with *R. ruffia* by Jumelle & Perrier de la Bâthie (1945). The study of Dransfield & Beentje (1995b) showed that the species in Madagascar is identical to *R. farinifera* in Africa and indeed they even considered that *Raphia* in Madagascar is introduced from Africa. The reasons for this are discussed fully in Dransfield & Beentje (1995b).

Ravenea – A genus endemic to Madagascar and Comoros. With the 20 currently known species, two species (*R. hildebrandtii* and *R. moorei*) are endemic to the Comoros. In fact, the genus was described first from a plant of *R. hildebrandtii* growing in the Botanic Gardens of Berlin in 1878 (Beentje 1994). The first species from Madagascar, *R. madagascariensis*, was described only in 1906 by Beccari. Among the twenty known species, the genus includes three species that have been classified previously in the genus *Louvelia*. This latter was established by Jumelle & Perrier de la Bâthie (1913) based on relatively superficial characters (e.g. squat palms for *Louvelia*, tree or erected palms for *Ravenea*; petals connate in *Louvelia*, free in *Ravenea*; fruits with apical stigmatic remains in *Louvelia*, lateral in *Ravenea*). The availability of new specimens and the discovery of several new species in recent decades showed that these criteria are frequently mixed and it was necessary to combine the two genera (Beentje 1994).

Satranala – A monotypic genus (type species: *S. decussilvae*) from the rainforest of the northeast Madagascar. The palm was discovered in 1992 by H. Beentje and differs from *Bismarckia nobilis* by its fruits with endocarp having conspicuous external wings rather than a shallowly grooved endocarp (Dransfield & Beentje 1995b).

Tahina – A monotypic and endemic genus (type species: *T. spectabilis*) that was discovered only in 2006 by Xavier Metz, beside an outcrop of karst limestone (Tsingy) in North-west of Madagascar. The posting of photographs of it

on the International Palm Society website by Bruno Leroy generated passionate discussion during several months among palm enthusiasts around the world. At first, thought to be a member of the Asian genus *Corypha*, examination of the herbarium specimen revealed its relationship with the genera *Chuniophoenix*, *Nannorrhops* and *Kerriodoxa* and its distinctness from all known genera (Dransfield et al. 2008b).

Voanioala – A monotypic and endemic genus (type species: *Voanioala gerardii*) belonging to Cocoseae. The existence of this palm had first been noted by M.E. Darian in 1984 based on loose endocarps and then described by Dransfield (1989) once complete collections had been made in the forests of Masoala in 1986.

Publication

Since the 19th century, five major publications on the palms of Madagascar have appeared and several taxonomic papers have been published especially during the last few decades.

The first book having a chapter dedicated to Madagascar palms was that of Henri Ernest Baillon : *Liste des plantes de Madagascar*, published between 1882 and 1895 (Dorr 1987). In this book, Baillon described eleven new species and seven new genera (*Dypsidium*, *Haplodypsis*, *Haplophloga*, *Neodypsis*, *Neophloga*, *Phlogella* and *Trichodypsis*).

The first book devoted to palms of Madagascar is *Palme del Madagascar descritte ed illustrate* of Odoardo Beccari (1906), in which the author compiled the fifty species and thirteen genera known at that time.

The second overview of Madagascar palms (Jumelle & Perrier de la Bâthie 1945), was a treatment in the series *Flore de Madagascar et des Comores*. This volume was based on the research done by the authors in Madagascar between 1900 and 1940. This edition treated eighteen genera and 115 palms species.

In 1995, Dransfield & Beentje released *The palms of Madagascar*, including sixteen genera and 171 species. The work of Dransfield & Beentje is based on detailed study of each herbarium specimen known at that time and represents thus the palms taxonomy that are currently accepted in Madagascar. In continuation of this book, Dransfield et al. (2006) published in 2006 *A field guide to the palms of Madagascar*, this new version including in addition new species that had been discovered since 1995.

Current knowledge of the Palm family

Despite significant progress being made in research on palms of Madagascar during the last three decades, the flora remains under-collected and our current knowledge is still incomplete. The exploration of new areas across the island resulted frequently in the discovery of new taxa. Between 1986 and 1995, during the preparation of *The palms of Madagascar*, Dransfield & Beentje discovered and described about eighty new species and three new genera. Five additional new species were discovered until 2006 and treated with the previous known species in the Field Guide (Dransfield et al. 2006). Since 2006, GIS techniques have been integrated in targeting areas for fieldwork. Such methods gave positive results during the ground truthing as new discoveries either

for undescribed taxa or populations have been made. Taxonomically, a new *Ravenea* has been described from Andilamena (Rakotoarinivo 2007), five new species of *Dypsis* from Makira (Rakotoarinivo et al. 2009), a new genus *Tahina* (Dransfield et al. 2008b) and recently fourteen new species from *Dypsis* and *Ravenea* discovered throughout the eastern region have been published (Rakotoarinivo & Dransfield 2010). From an ecological point of view, recent fieldwork allowed the discovery of new populations of some species, such as *Dypsis ambanjae*, *D. coursii* and *D. tanalensis*, the last collections of which were made in the 1950's or even at the beginning of the 20th century. Nowadays, only a small part of the forests of Madagascar has been visited so far and at the same time access to primary vegetation becomes more and more difficult following deforestation (electronic appendix 4). It is predicted that complementary research in those unexplored areas will bring new knowledge on palms of Madagascar as many species remain poorly known. Figure 2 illustrates the relationship between the number of collections and the number of species. On average, half of the known species have been collected between twice and ten times while twenty species have been collected only once. Hence the occurrence of some species in the wild remains uncertain because the last time they were collected was several decades ago or because they occur in areas generally well-worked by botanists. For instance, *Ravenea latisecta* was described from the Andasibe area but this palm has not been collected since 1991, and even this collection is doubtfully determined while the area is one of the most visited in Madagascar. Conversely, Tsaratanana massif in the north of Madagascar is not well explored botanically and the few species endemic to the area are only known from single type specimens, e.g. *Dypsis ankaizinensis*, *D. canescens*, *D. ligulata* and *D. tsaratananensis*.

Our current knowledge of the palms of Madagascar relies on field observation and herbarium specimens. Herbarium specimens are, as expected, available for consultation in the major herbaria already cited earlier. With advances in technology, information on the specimen labels or even the images of some specimens are also accessible on-line through different data portals such as Herbat of Kew Gardens (<http://apps.kew.org/herbat/navigator.do>), Tropicos of Missouri Botanical Garden (<http://www.tropicos.org/>), Sonnerat of Musée National d'Histoire Naturelle, Paris (<http://coldb>).

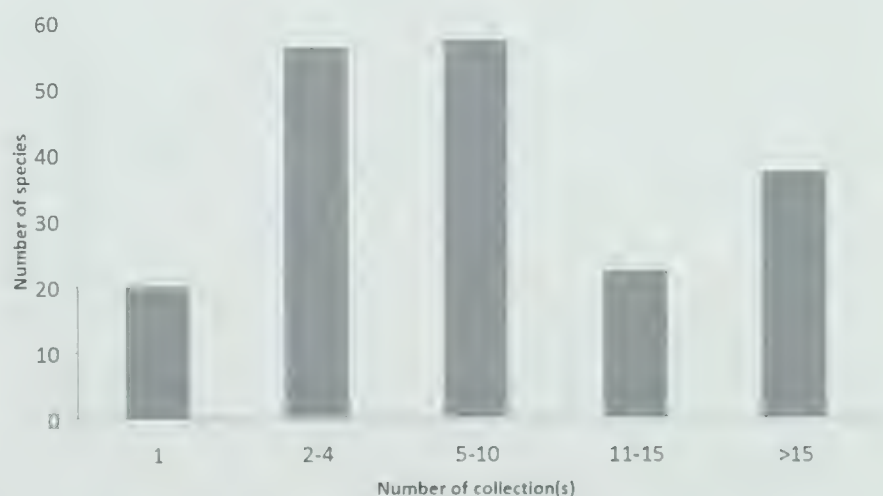


Figure 2 – Relationship between frequency of collection and the number of species.

mnhn.fr/colweb/form.do?model=SONNERAT.wwwsonnerat.wwwsonnerat.wwwsonnerat) or the international project GBIF (<http://data.gbif.org/welcome.htm>).

Palms are among the most popular plants in horticulture, resulting in the exploitation of the palms as hundreds of thousands are sold annually for home use (Gibbons 2003). Given the high diversity of palms in Madagascar, the island has provided several species for worldwide horticulture. Among the most popular species from Madagascar are *Dypsis lutescens*, *D. decaryi*, *Bismarckia nobilis*, *Marojejya darianii*, *Ravenea rivularis* and *Lemurophoenix halleuxii*, but in fact there is an almost insatiable demand for seeds of any Madagascar palm. Palms are mostly exported as seeds from Madagascar. At the moment, the international trade of ten species is regulated under CITES convention (<http://www.cites.org/eng/resources/species.html>) while the exportation of the remaining species requires only special permits from the Ministry of Water and Forests in Madagascar. As expected, a major part (if not all) of these exported seeds originate in the wild. The collections of seed has caused the decline of the population of some species since palm trees are frequently chopped down in order to access the fruits (e.g. Ratsirarson et al. 1996), thus seriously compromising regeneration. On the other hand, some species are known only from protected areas but poaching always happens even when access is regulated and the site is often remote. However, horticulture also brings benefits to our knowledge of palms in Madagascar. Thanks to seed collectors, new locations, new forms of a given species or even new species have frequently been highlighted. At the moment, a host of different forms of several species exist in horticulture, thus generating great discussion among palms enthusiasts as to whether some should be considered as new species. So far, six palm species have been described from samples cultivated outside Madagascar. These are *Dypsis albofarinosa*, *D. cabadae*, *D. carlsmithii*, *D. leptocheilos*, *D. plumosa* and *D. robusta*. These species may have been exported as seed with incorrect identification and information related to their exact origin has been lost over time. Today, all but *D. plumosa* and *D. cabadae* have been discovered in their natural habitat in Madagascar and *D. cabadae* seems almost certainly to be native to the Comoros.

All this obvious progress in taxonomy is still insufficient in resolving the relationships between the genera (*Dypsis*, *Lemurophoenix*, *Masoala* and *Marojejya*) within subtribe Dypsidinae. Molecular study suggests that the tribe is monophyletic but with low support (Dransfield et al. 2008a). In contrast, the study of Baker et al. (2011) indicates that the genus *Dypsis* may not be monophyletic. Such conclusions emphasize the necessity for an intensive analysis in the relationship between the genera of the Dypsidinae, and especially the relationships between the species of *Dypsis*. As stated before, the proportion of explored areas for palms still remains small compared to the current extent of primary vegetation in Madagascar. As more new material becomes available, more progress in the knowledge of palms in Madagascar and their relationships with those in other territories will develop.

In general, palms are highly threatened in Madagascar. The latest conservation analysis shows that only eighteen species do not fill one of the IUCN criteria of threat (Rako-

toarinivo 2008). Habitat loss and degradation, together with selective exploitation constitute the main threats for palms. Some species are no longer found at their type locality, others have faced population decline during the last decades so only few mature individuals persist in the wild. Their survival becomes critical. It is recommended thus that botanists and scientists keep exploring for palms in Madagascar and focusing their research mostly in taxonomy, ecology and genetics. Recent study on the biogeography of palms in Madagascar (Rakotoarinivo 2008) demonstrated that turnover of palm flora can be pronounced between two sites. Almost all of the species have narrow distribution ranges and the prediction of the distribution of rare species is usually difficult. Of course, the area around the bay of Antongil and Masoala Peninsula have for a long time been supposed to have the greatest diversity in general palm flora and frequency of rarities. However, the recent discovery of *Tahina spectabilis* in the dry area of Madagascar and the unexpected emergence of several un-described taxa during the last few years has called into question the way sites have been targeted for fieldwork. Trends show that every piece of eastern forest may contain rare or poorly known species. To assess completely the knowledge of palms in Madagascar, it is recommended to continue the survey both in remote areas and in places that have already been visited but are supposed still to be incompletely surveyed.

CONCLUSIONS

The palm family displays a high rate of diversity and especially high rate of endemism in Madagascar. Palms species are three times more diverse in Madagascar compared to the continent of Africa and 98% of the known 195 species occur only in the island. With the high rate of deforestation, habitat degradation or selective exploitation, palms have become highly threatened in Madagascar. In fact, palms are among the most important natural resources for the daily livelihood of villagers living near forests in Madagascar. Palms may also be a source of money from the selling of their seeds. Unfortunately, such practices have led to the loss and decline of many populations to the extent that the survival of several species becomes threatened. Many NGOs and public institutions run different programs for saving the most threatened species in their region. One thing has been proven during the last few years and that is that our knowledge of palms still remains incomplete. The result of intensive fieldwork during the last decades demonstrates that exploration of new sites has allowed the discovery of new taxa and the rediscovery of some species thought to be extinct. Compared with the extent of the remaining humid forest of Madagascar, the area surveyed for palms is small and many areas of Madagascar remain unexplored. With the expansion of general plant collecting all over Madagascar, new samples are becoming available and species thought to be rare or endemic to a single site are thus being recorded from additional locations. A plea is made to general collectors to continue to make collections of palms. Gathering information on palms and making it available to scientists or conservation decision-maker becomes ever more important as the preservation strategy depends mainly on ecological data at the population level.

The more we know about the palms and their populations, the easier it becomes to develop strategies to protect the severely threatened species.

SUPPLEMENTARY DATA

Supplementary data are available in pdf at the Supplementary Data Site of publications from the National Botanic Garden of Belgium (<http://www.nbgpublisher.be> > SBB50 > folder 519) and consist of the following: (1) list of the top ten researchers who collected palms in Madagascar; (2) photographs of main botanists having worked on palms of Madagascar; (3) evolution of palm collections throughout the years; (4) distribution of palm collections in Madagascar compared to vegetation types.

ACKNOWLEDGEMENTS

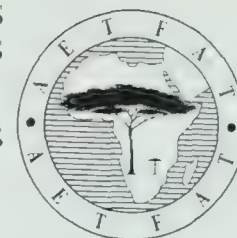
We express our gratitude to our colleague Dr William J. Baker for his help in compiling documents related to this topic. We are thankful to two anonymous reviewers for the constructive criticism they provided to improve this paper.

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Manuscript received 15 Sep. 2010; accepted in revised version 22 Feb. 2012.

Communicating Editor: Thomas Haevermans.



A brief history of *Aloe* discovery and popularisation in southern Africa

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Background – The discovery, description and popularisation of aloes from southern Africa (here defined as Namibia, Botswana, Swaziland, Lesotho and South Africa) has not progressed in a linear manner since the region first started receiving the attention of botanists and plant collectors during the late 17th century. New species of *Aloe* continue to be recognised and described in the 21st century.

Methods – We track the above historical aspects in relation to several factors: geographic access, horticultural interest, production of accessible, popular books, and the efforts of highly productive individuals such as Gilbert Westacott Reynolds. The influences of his and subsequent illustrated works are considered, particularly as catalysts of further research and botanical exploration in the region.

Results – An analysis of taxa distribution patterns in relation to collector attention and terrain diversity reveals historically overlooked locales which may yet yield further new species.

Key words – *Aloe*, Asphodelaceae / Aloaceae, botanical exploration, history, Reynolds, southern Africa.

INTRODUCTION

The Flora of southern Africa region (FSA: Namibia, Botswana, Swaziland, Lesotho and South Africa) harbours ± 150 members of the genus *Aloe* L., of which around 114 are endemic to the region (Aloes of the World Database 2010). Undoubtedly the foremost researcher on southern African aloes in the modern era is Gilbert Westacott Reynolds (1895–1967). His interest in the group began in about 1930 when he collected his first aloe. In the ensuing twenty years, he travelled over 170,000 km in southern Africa to study and photograph aloes in the wild, all the while collecting herbarium specimens (Walker 2010). This passion for aloes resulted in the publication of a seminal work on the genus, *The Aloes of South Africa* (Reynolds 1950, with three later editions), which covered in detail the 133 aloes then recognised regionally. Reynolds described 26 new aloes from the FSA region that are still regarded as current taxa and with a total of 102 new names published by him for the genus; he was the most prolific publisher of *Aloe* names of all time (Walker 2010). He did not stop his investigation of aloes at the borders of southern Africa, but continued to travel and study them throughout their distribution range. He ultimately produced a

total of 122 publications, eight of which were books (Walker 2010). He followed his monumental work *The Aloes of South Africa* with a similarly-styled and complementary publication titled *The Aloes of Tropical Africa and Madagascar* (Reynolds 1966).

This article summarises our perspective on the influences of publications by Reynolds, and subsequent illustrated works by other authors, particularly as catalysts of further research and botanical exploration in the region. Furthermore, an analysis of taxa distribution patterns in relation to terrain diversity and previous collector attention is presented that reveals historically overlooked locales which may yet yield further new species.

PRE 1950

Prior to 1900, a total of 195 names had been published in the genus *Aloe* for plants from southern Africa. However, a mere 43 of these are still regarded as good taxa. In the fifty years (1901–1950) prior to the publication of *The Aloes of South Africa* (Reynolds 1950) a further 149 new *Aloe* names were published for the region, with 81 of these still current. During this period there were six prominent students of the

genus *Aloe* in southern Africa who, between them, published 124 new names, of which 76 are still regarded as current (table 1). Reynolds is, unsurprisingly, foremost amongst these authors.

It was at the beginning of the 20th Century that Alwin Berger (1871–1931), then Curator of Sir Thomas Hanbury's famous La Mortola Gardens near Ventimiglia in Italy, published monographic treatments of the genus (Berger 1905, 1908). An amended form of his proposed infrageneric classification for *Aloe* has survived to the present day, mainly because it was adopted by Reynolds (1950) in his influential publications (Figueiredo & Smith 2010).

POST 1950

On completion of his fieldwork in southern Africa, and in writing up his authoritative work in 1950, Reynolds wrote (p. 67): "The aloes of South Africa have, it seems, been well investigated, and it does not appear that many – if any – new species still remain to be discovered in South Africa". This was a rather bold statement to make and he was indeed proven to be very wrong. However, the gravity with which such a statement from the meticulous and highly respected expert on the genus would have been taken likely lulled taxonomists into a false sense of finality on the taxonomy and diversity of the regional group. Accordingly, in the decade following Reynolds (1950) only one species, *A. modesta* Reynolds, was additionally described. However, *Aloe* scholars eventually awoke to remaining opportunities and in the fifty years (1951–2000) following publication of his book, a further 26 new names were published for southern Africa. Twenty three of these still upheld as current taxa (fig. 1). Notably, only one of these new names was published by Reynolds, who post-

1950 almost wholeheartedly dedicated his attention to aloes found elsewhere in Africa, and Madagascar.

The past decade (2001–2010) has seen the publication of a further thirteen new *aloe* names (all still current) in the FSA region (fig. 1). It is during this recent period, and to some extent the latter half of the 20th century, that joint authorship of new *Aloe* names has become more common practice: seventeen new names published since 1950 were authored by more than one person. The most productive authors during this period are detailed in table 2.

POPULAR ALOE BOOKS POST 1950

The publication of *The Aloes of South Africa* (Reynolds 1950) sparked an interest in aloes that would last for many decades. Arguably the book published in Afrikaans by Groenewald (1941) had primed this interest, albeit within a more restricted sector of society and academia. Aloes quickly gained horticultural interest and are still valued as feature plants, especially for gardens in areas where water is scarce. This ongoing enthusiasm has been fuelled by other illustrated works from various authors that have acted as catalysts for further research on the group, and botanical exploration within the region. These works include:

- *What aloe is that?* (Judd 1967)
- *South African aloes* (Jeppe 1969)
- *Aloes of the South African veld* (Bornman & Hardy 1971)
- *Aloes of South-West Africa* (Jankowitz 1975)
- *Guide to the aloes of South Africa* (Van Wyk & Smith 1996)
- *Aloe in Flora of Southern Africa* (Glen & Hardy 2000) [technical publication]

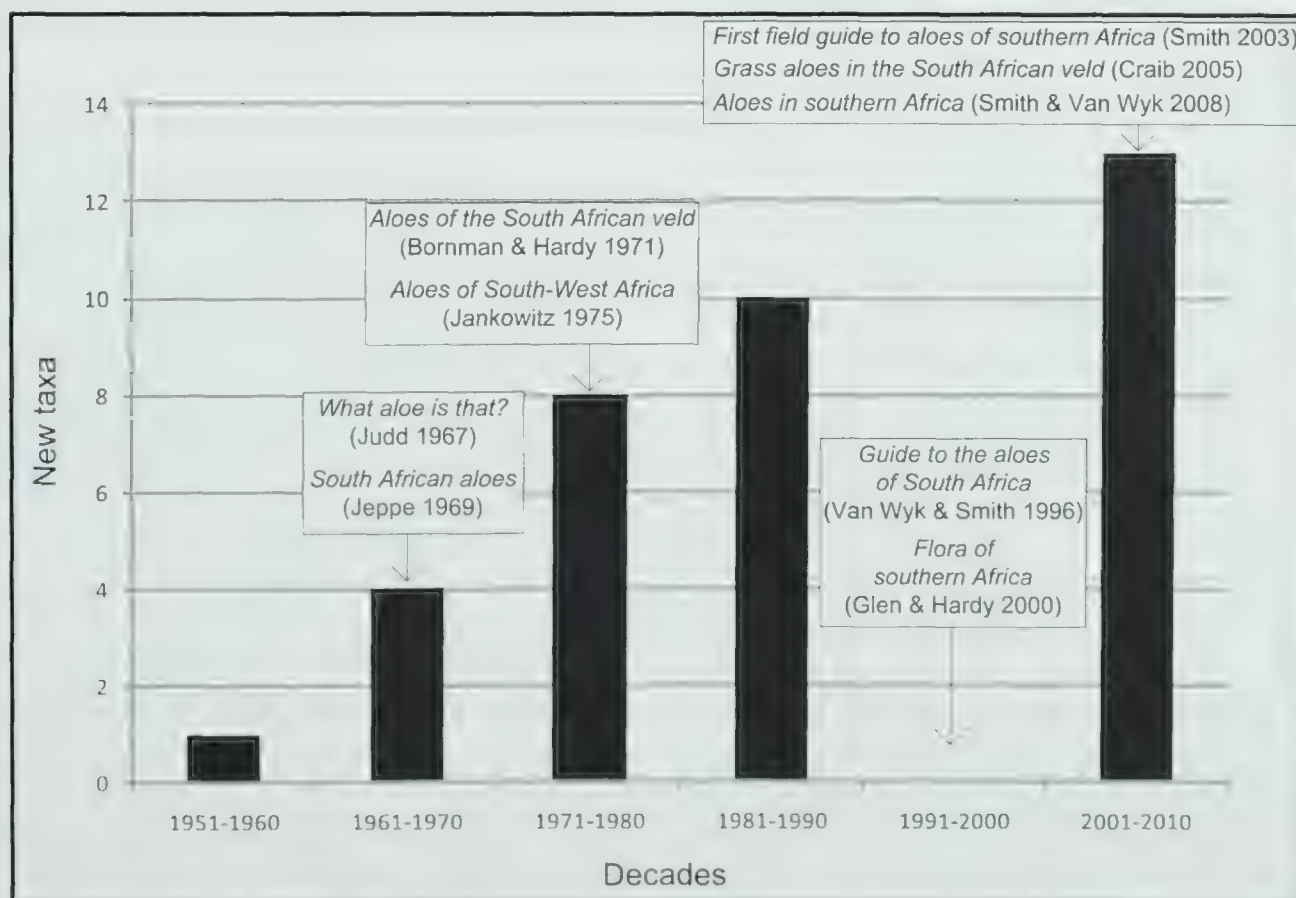


Figure 1 Number of new *Aloe* taxa (still regarded as current) described for southern Africa in the six decades since publication of Reynolds' *The Aloes of South Africa* in 1950. Other milestone publications on the genus are also plotted on the graph to indicate the effect such publications have had on sustaining and driving an interest in the genus, reflected in the subsequent discovery and description of new taxa.

Table 1 – Six most productive authors of *Aloe* names from the FSA region between 1900 and 1950.

Researcher	Protologue date ranges	Names published	Current taxa
S. Schonland	1903–1911	19	10
A. Berger	1904–1922	24	12
I.B. Pole Evans	1914–1938	18	14
N.S. Pillans	1928–1939	11	9
B.A. Groenewald	1935–1939	14	6
G.W. Reynolds	1936–1950	38	25

- *First field guide to aloes of southern Africa* (Smith 2003)
- *Grass aloes in the South African veld* (Craib 2005)
- *Aloes in southern Africa* (Smith & Van Wyk 2008)

When the publication of these books is plotted on a graph showing the number of aloes described per decade (fig. 1), it becomes apparent that these publications possibly play a major part in sustaining and revitalising the interest in aloes, in both lay and scholarly sectors. Reference works available in print – especially well-illustrated ones – enable the ready identification of novelties and their subsequent referral to scientists for description. In the decade following such a publication, one sees an increase in the number of new taxa described. Conversely, no new books on aloes appeared during the period 1981–1990, and no *Aloe* taxa were described in the subsequent decade (1991–2000). It could, however, merely be coincidence as there are several other factors that may also influence this phenomenon.

TAXA DESCRIBED SINCE 1950

The 36 new aloes described since 1950 (that are still regarded as current taxa in the Aloes of the World Database) can be divided into four main categories, with several species falling into more than one of these (table 3). The four categories are:

- *Cryptic taxa*: these are aloes that are easily overlooked. Most grass aloes fall into this category since they usually have deciduous leaves and flower during the summer months. They are thus not obvious during the winter when most people would expect to find aloes flowering in the veld. Very small aloes also fall into this category. They invariably grow in rock crevices and under other plants and are thus easily overlooked. Their leaves also possess cryptic colouration, with spots or blotches that well camouflage them.
- *Localised taxa*: these are aloes that have a very restricted distribution range. Aloes in general tend to have rather small distribution ranges, but taxa that fall into this category are usually restricted to a very small area or mostly only one or two subpopulations. Many of these also grow in remote and often inaccessible areas and this explains why they were not discovered earlier, as they would have been bypassed by Reynolds in the course of his travels (see Reynolds 1950: map p. 68). Their discovery has often been more by luck than design.
- *Cremnophytes*: these are aloes that grow on sheer rock faces. This type of habitat is not accessible to most peo-

Table 2 – Six most productive authors of *Aloe* names from the FSA region in the period 1950–2010.

Researcher	Protologue date ranges	Names published	Current taxa
I.C. Verdoorn	1961–1979	4 (1 with D.S. Hardy)	4
W. Giess	1970–1974	3 (1 with H. Merxmüller)	3
J.J. Lavranos	1971–1973	3	2
D.S. Hardy	1971–1987	7 (3 with H.F. Glen; 1 with I.C. Verdoorn)	7
E.J. van Jaarsveld	1981–2009	11 (6 with various co-authors)	11
G.F. Smith	2003–2010	5 (2 with N.R. Crouch; 2 with R.R. Klopper)	5

- ple and it is only the avid rock climber that will be able to reach and examine these plants. Many cremnophytes are also very localised and thus fall into the previous category as well.
- *Taxonomically challenging*: these are aloes that are difficult to classify and describe, or where there are differences in opinion as to the status of the taxon. Many of them belong to the maculate group, which are notoriously difficult to identify and order.

FUTURE DISCOVERIES

Holland (1978) found that species diversity across the range of the genus *Aloe* increases directly with terrain diversity: 50% of genus diversity could be explained by this environmental variable. The terrain diversity of Holland (1978) was given as a function of local relief, degree of dissection of terrain, steepness or otherwise of slopes and the complexity of the array of slope facets. Two zones of high terrain diversity were shown by Holland (1978) for southern Africa; the first centred on the eastern seaboard, and the second on northern Namaqualand and the Richtersveld.

When, for southern Africa, one overlays these areas of high terrain diversity on a map detailing the number of *Aloe* taxa recorded per quarter degree grid square, a correlation is evident (fig. 2). Effectively, Holland (1978) predicted the site of discovery of new *Aloe* species on the West coast, for most discoveries there have been made subsequent to his publication. Northern Namaqualand and especially the Richtersveld area are fairly rich in aloes that are localised and endemic or near-endemic to this extremely arid and remote region. However, one anticipates that further aloes will be discovered here, based on its high terrain diversity and the limited exploration to date.

In considering fig. 2, there are some regions of high taxon diversity along the eastern seaboard and particularly along the eastern escarpment in Mpumalanga and Limpopo, but there is an obvious gap in the northern part of the Eastern Cape Province. This area of high terrain diversity is, based on collections to date, very poor in aloes. Although histori-

Table 3 – Characteristics of *Aloe* species discovered in southern Africa since 1950.

Taxon by decade, and year of protologue	Cryptic	Localised	Cremnophytes	Taxonomically challenging
1951–1960				
<i>A. modesta</i> Reynolds (1956)	•	•		
1961–1970				
<i>A. monotropa</i> I.Verd. (1961)		•		•
<i>A. soutpansbergensis</i> I.Verd. (1962)	•	•		
<i>A. prinslooii</i> I.Verd. & D.S.Hardy (1965)				•
<i>A. namibensis</i> Giess (1970)		•		
1971–1980				
<i>A. buhrii</i> Lavranos (1971)		•		
<i>A. erinacea</i> D.S.Hardy (1971)		•		•
<i>A. esculenta</i> L.C.Leach (1971)				•
<i>A. chlorantha</i> Lavranos (1973)		•		
<i>A. dewinteri</i> Giess (1973)			•	
<i>A. argenticauda</i> Merxm. & Giess (1974)				•
<i>A. pictifolia</i> D.S.Hardy (1976)		•	•	
<i>A. corallina</i> I.Verd. (1979)			•	
1981–1990				
<i>A. dabenorisana</i> Van Jaarsv. (1981)			•	
<i>A. meyeri</i> Van Jaarsv. (1981)			•	
<i>A. reitzii</i> Reynolds var. <i>vernalis</i> D.S.Hardy (1981)		•		
<i>A. komaggasensis</i> Kritz. & Van Jaarsv. (1985)		•		
<i>A. inconspicua</i> Plowes (1986)	•	•		
<i>A. cooperi</i> Baker subsp. <i>pulchra</i> Glen & D.S.Hardy (1987)	•	•		•
<i>A. fouriei</i> D.S.Hardy & Glen (1987)	•			
<i>A. hardyi</i> Glen (1987)		•	•	
<i>A. marlothii</i> A.Berger subsp. <i>orientalis</i> Glen & D.S.Hardy (1987)				•
<i>A. ciliaris</i> Haw. var. <i>redacta</i> S.Carter (1990)		•		•
2001–2010				
<i>A. craibii</i> Gideon F.Sm. (2003)	•	•		
<i>A. kouebokkeveldensis</i> Van Jaarsv. & A.B.Low (2004)		•		
<i>A. omavandae</i> Van Jaarsv. & A.E.van Wyk (2004)			•	
<i>A. arborescens</i> Mill. subsp. <i>mzimnyati</i> Van Jaarsv. & A.E.van Wyk (2005)		•	•	
<i>A. chalissii</i> Van Jaarsv. & A.E.van Wyk (2006)	•		•	•
<i>A. kaokoensis</i> Van Jaarsv., Swanepoel & A.E.van Wyk (2006)		•		
<i>A. vanrooyenii</i> Gideon F.Sm. & N.R.Crouch (2006)				•
<i>A. pavelkae</i> Van Jaarsv., Swanepoel, A.E.van Wyk & Lavranos (2007)			•	
<i>A. juddii</i> Van Jaarsv. (2008)		•		
<i>A. hahnii</i> Gideon F.Sm. & Klopper (2009)				•
<i>A. kannelii</i> Van Jaarsv. (2009)		•		
<i>A. neilcrouchii</i> Klopper & Gideon F.Sm. (2010)		•		•
<i>A. nicholsii</i> Gideon F.Sm. & N.R.Crouch (2010)	•	•		•

cally quite remote and fairly inaccessible, the improvement in road infrastructure in recent years allows much better access. Further exploration in this region will undoubtedly lead to the discovery of new aloes.

Most *Aloe* novelties represented by herbarium specimens have been described; although taxonomic problems still exist in a few groups, most notable of which are the maculates

and some populations of members of *Aloe* Section *Purpurascens* Salm-Dyck. Further new descriptions are likely to flow from active fieldwork in rugged environments. In venturing forth in a directed manner botanists should bear in mind the statement by Reynolds that “...the little botanical knowledge that [I] have managed to acquire [on *Aloe*] has been gained the hard way – in the veld.”

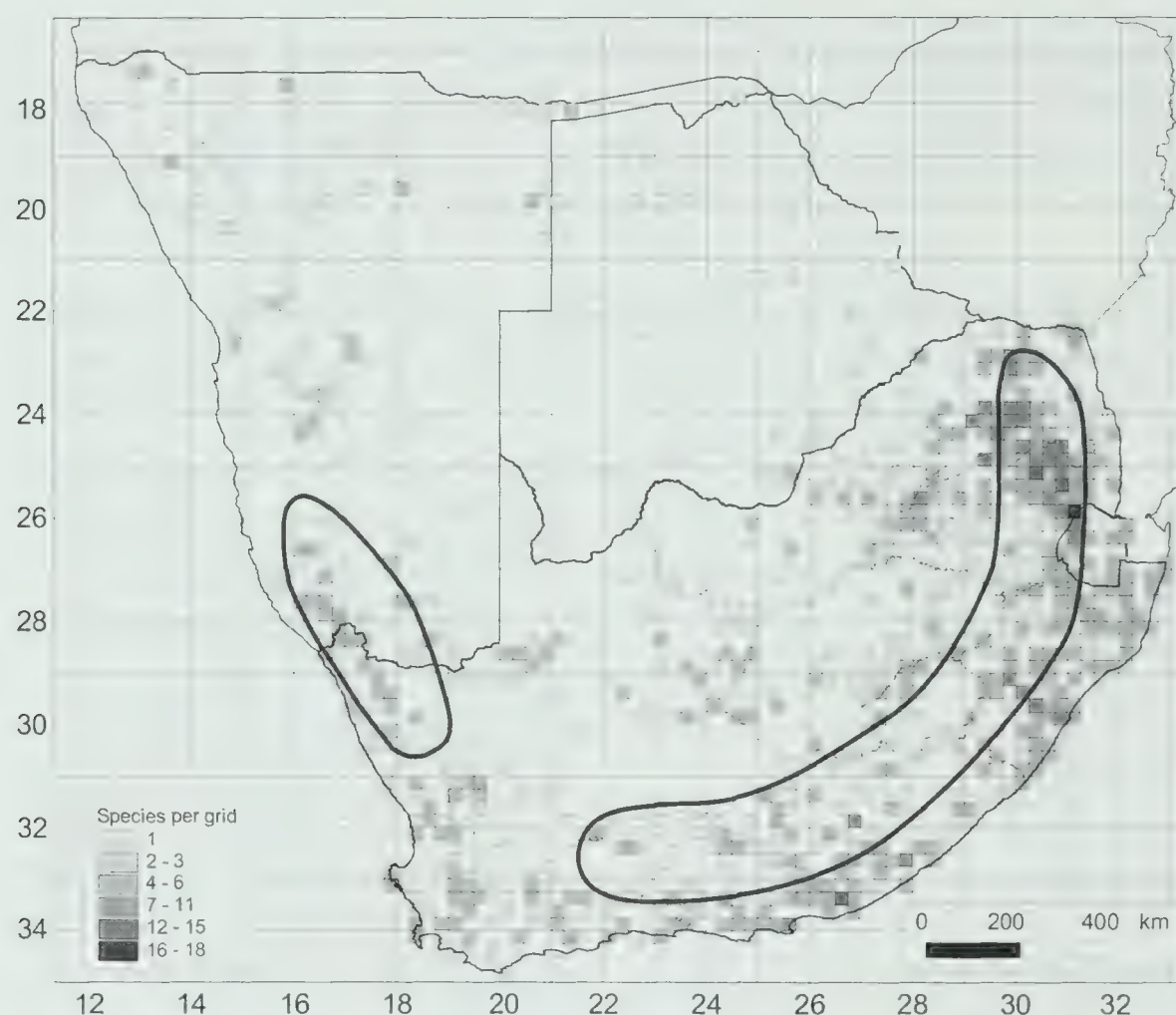


Figure 2 – Number of *Aloe* taxa per quarter-degree grid square in southern Africa, with an overlay of the two areas of high terrain diversity identified by Holland (1978), indicated by closed loops.

ACKNOWLEDGEMENTS

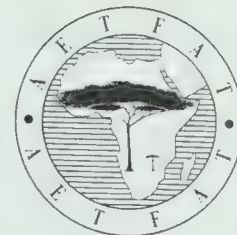
The Andrew W. Mellon Foundation is thanked for financial assistance that has enabled the Aloes of the World project. Ms Hester Steyn, National Herbarium, South African National Biodiversity Institute is thanked for producing the map showing *Aloe* diversity per unit area. For assistance in the field that has resulted recently in the discovery of new *Aloe* species we are grateful to Mrs Isabel Johnson, Mr Geoff Nichols, Mrs Sharon Louw and Mr Gareth Chittenden; Mr Ben Botha of Winston Park has played a significant role as an expert grower of newly found taxa. We also thank two referees for suggesting improvements to the manuscript.

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Manuscript received 30 Sep. 2010; accepted in revised version 3 Feb. 2011.

Communicating Editor: Rainer Bussmann.



Phylogenetic relationships of Malagasy Hyacinthaceae

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Background – Whereas subfamily Oziroeoideae of the petaloid monocot family Hyacinthaceae is restricted to South America, the three other subfamilies, Ornithogaloideae, Urgineoideae and Hyacinthoideae, have much larger primary distribution areas spanning the Mediterranean and Central Europe, Arabian Peninsula, Indian subcontinent, Far East (China and Japan) and Africa, with some members also in Madagascar. Based mainly on morphology, until recently, most of the Malagasy species have been included in genera found also outside this island. Morphological characters alone have been misleading in many cases, resulting in erroneous generic classifications.

Method – Analysis of plastid DNA sequences was used to reconstruct phylogenetic relationships among members of old world Hyacinthaceae.

Key results – Phylogenetic analysis based on multiple plastid DNA markers has changed our views substantially, leaving many of the Malagasy Hyacinthaceae taxa as monophyletic groups. All Malagasy members of Urgineoideae form a well-supported clade (*Rhodocodon*/*Drimia cryptopoda*) pointing to a single colonization from continental Africa. *Drimia cryptopoda* is a morphologically deviant species previously misplaced in *Hyacinthus*. The Urgineoideae from India do not appear to be directly related to African or Malagasy species, but show close relationships to the Mediterranean *Urginea* s. str. Two members of Hyacinthoideae are present in Madagascar. One of them, *Ledebouria* sp. ined., is related to South African species, whereas the other, *L. nossibeensis*, shows strong relationships to *L. hyacinthina* from India and to *L. grandifolia* from Socotra. *Dipcadi* (Ornithogaloideae) forms a well-supported monophyletic clade.

Conclusion – We presume a single colonization from mainland Africa followed by rapid radiation in different habitats in Madagascar. The close relationship of Indian *Dipcadi* with those of the Mediterranean points to a Northern Hemisphere migration route linking India and the Mediterranean and possibly involving also the Arabian Peninsula.

Key words – Hyacinthaceae, phylogeny, DNA sequence analysis.

INTRODUCTION

The division of the Hyacinthaceae into the four subfamilies Oziroeoideae, Urgineoideae, Ornithogaloideae, and Hyacinthoideae (Pfosser & Speta 1999, Manning et al. 2004, 2009, Wetschnig et al. 2007) is now well accepted. It is supported by morphological, chemotaxonomical, and molecular data alike. Hyacinthaceae occurs in South America (Oziroeoideae only), in Africa south and north of Sahara, in Madagascar, Arabian Peninsula, and India (Urgineoideae, Ornithogaloideae, and Hyacinthoideae). The latter three subfamilies share a secondary center of diversity spanning the Mediterranean and Eurasian floristic regions. A single iso-

lated group of species is found in SE Asia (*Barnardia* of subfamily Hyacinthoideae; Speta 1998a, 1998b, Pfosser & Speta 1999, Pfosser et al. 2003).

It has been suggested that the involvement of species from South Africa, South America, and Madagascar in the basal branching patterns of subfamilies and tribes indicates a southern, probably Gondwanan, origin of Hyacinthaceae (Pfosser & Speta 1999). This hypothesis implies that major lineages diverged from each other in Gondwana and were separated later by continental break-up. Taxa rafting on the Palaeo-Indian plate as it moved northwards play a key role in this hypothesis. Similar northward transport via India

has been inferred in plant families such as Crypteroniaceae (Conti et al. 2004, Rutschmann et al. 2004), Dipterocarpaceae (Ashton & Gunatilleke 1987, Ducousso et al. 2004), but also for animals such as acrodont lizards (Macey et al. 2000), ranid frogs (Biju & Bossuyt 2003), caecilian amphibians (Wilkinson et al. 2002), and ratite birds (Cooper et al. 2001). Alternatively, the present distribution of Hyacinthaceae could be explained by more recent long-distance dispersal across the Indian Ocean and/or by migration from the Mediterranean and Arabian regions towards India.

Historical biogeographic reconstruction based on phylogenetic analysis is an important way to understand the evolutionary history of organisms in space and time. In order to test the possible involvement of India as a raft for the northwards transport, we have sampled palaeotropic taxa present in southern Africa, Madagascar, India, Arabian Peninsula, and in the Mediterranean, with emphasis on *Drimia/Rhodocodon* (Urgineoideae), *Dipcadi* (Ornithogaloideae) and *Ledebouria* (Hyacinthoideae) because of their large distribution areas. In addition, we included representative members for each subfamily in order to position the target genera in a phylogenetic framework.

MATERIALS AND METHODS

Taxonomic sampling

Species and lineages sampled are listed in the electronic appendix. Sampling focused on lineages having representatives in South Africa, Madagascar and India, including their closest relatives from other areas. Information for this selection was taken from the literature (Pfosser & Speta 1999, Pfosser et al. 2003, 2006, Manning et al. 2004, 2009) and from own data.

Molecular techniques, DNA data generation

DNA was extracted from leaf tissue using either the DNeasy Plant Mini Kit (Qiagen, Valencia, California, USA) or the CTAB method (Doyle & Doyle 1987) with modifications (Pfosser et al. 2006). The *trnC^{GCA}-ycf6* intergenic region was sequenced for this study. Primers used for amplification were *trnC^{GCA}F* (CCA GTT CRA ATC YGG GTG) (modified from Demesure et al. 1995) and *ycf6R* (GCC CAA GCR AGA CTT ACT ATA TCC AT) (Shaw et al. 2005) using standard thermal cycling conditions (95°C, 5 min; 35 cycles of 94°C, 20 sec; 50°C, 30 sec; 72°C, 1 min; final extension at 72°C, 10 min). PCR was performed using Hybaid thermal cyclers in 20 µL volumes with the following reaction components: 2 µL template DNA (10–100 ng), 2X DreamTaq ReadyMix PCR reaction mix (Fermentas) and 0.1 µmol/L each primer. Amplified double-stranded DNA fragments were purified with Exonuclease I and Shrimp alkaline phosphatase (Fermentas) following the protocol of the manufacturer to remove unincorporated nucleotides and excess primers prior to sequencing. Dideoxy sequencing was performed using the purified PCR fragments following the DYEnamicET cycle sequencing protocol (General Healthcare, USA). Both strands were sequenced using the same primers as for amplification. Separation of fragments and base calling was performed on a MegaBace 500 automated sequencer (General

Healthcare, USA). On average, less than 1% of data matrix cells were scored as missing data.

All sequences have been deposited in the EMBL database (for accession numbers, see electronic appendix). Clustal X (Jeanmougin et al. 1998) was used for automatic DNA sequence alignment. Final alignment was done by eye in order to homogenize the positions of insertion/deletion mutations (indels). Indels in the data matrix were coded as additional characters using the simple indel coding approach (Simmons & Ochoterena 2000) implemented in the computer program GapCoder (Young & Healy 2003). The aligned data matrices were 1166, 1108, and 1152 nucleotide positions long for Urgineoideae, Ornithogaloideae and Hyacinthoideae, respectively. Ambiguous and incomplete regions at the beginning and end of sequences were excluded from the analysis: positions 1–48 and 1112–1166 for Urgineoideae, 1–51 and 1044–1108 for Ornithogaloideae, and 1–49 and 1051–1152 for Hyacinthoideae. An AT-rich region resulting in ambiguous alignments at positions 490–540 in Urgineoideae was excluded from the analysis alike. The aligned indel blocks consisted of 102, 113, and 95 positions for Urgineoideae, Ornithogaloideae and Hyacinthoideae, respectively.

Tree searches were performed using the nucleotide data together or without the indel data. Phylogenetic analysis using the maximum parsimony (MP) method were performed with the computer program PAUP* version 4.0b10 (Swofford 2000). Most parsimonious trees were obtained by 1000 replicates of random sequence addition using tree bisection-reconnection (TBR) branch swapping under the Fitch criterion (Fitch 1971). Ten thousand fast bootstrap replicates (Felsenstein 1985) were used to assess confidence limits for the resulting tree topologies.

RESULTS AND DISCUSSION

The phylogenetic trees (figs 1–3) resulting from *trnC^{GCA}-ycf6* data match topologies obtained from earlier analyses of different cpDNA regions (Pfosser & Speta 1999, 2001, 2004, Pfosser et al. 2003, 2006, Manning et al. 2004, 2009, Wetschnig et al. 2002, 2007). Also extended taxa sets matching taxon sampling from previous analyses yielded results consistent with previous analyses. As the main focus of this study was to establish a phylogenetic framework for genera distributed in an area spanning from Africa, via Madagascar and Arabian Peninsula to India (*Rhadamanthus/Rhodocodon/Drimia cryptopoda*, *Ledebouria*, *Dipcadi*), most clades not related to our study groups were excluded from the analyses. However, a much broader sampling of taxa from Madagascar and India compared to previous analyses, as well as the high amount of sequence divergence of the *trnC^{GCA}-ycf6* region in Hyacinthaceae, helped to improve the resolution in our study groups.

In agreement with previous studies (Pfosser & Speta 1999, 2001, 2004, Pfosser et al. 2003, 2006, Manning et al. 2004, 2009, Wetschnig & Pfosser 2003, Wetschnig et al. 2007), analysis of the *trnC^{GCA}-ycf6* region yielded evidence for *Bowiea* being sister to the remaining taxa in Urgineoideae and *Pseudoprospero* being sister to all other members of Hyacinthoideae. Therefore, *Bowiea* and *Pseudoprospero* have been used as outgroups for the remaining Urgineoideae

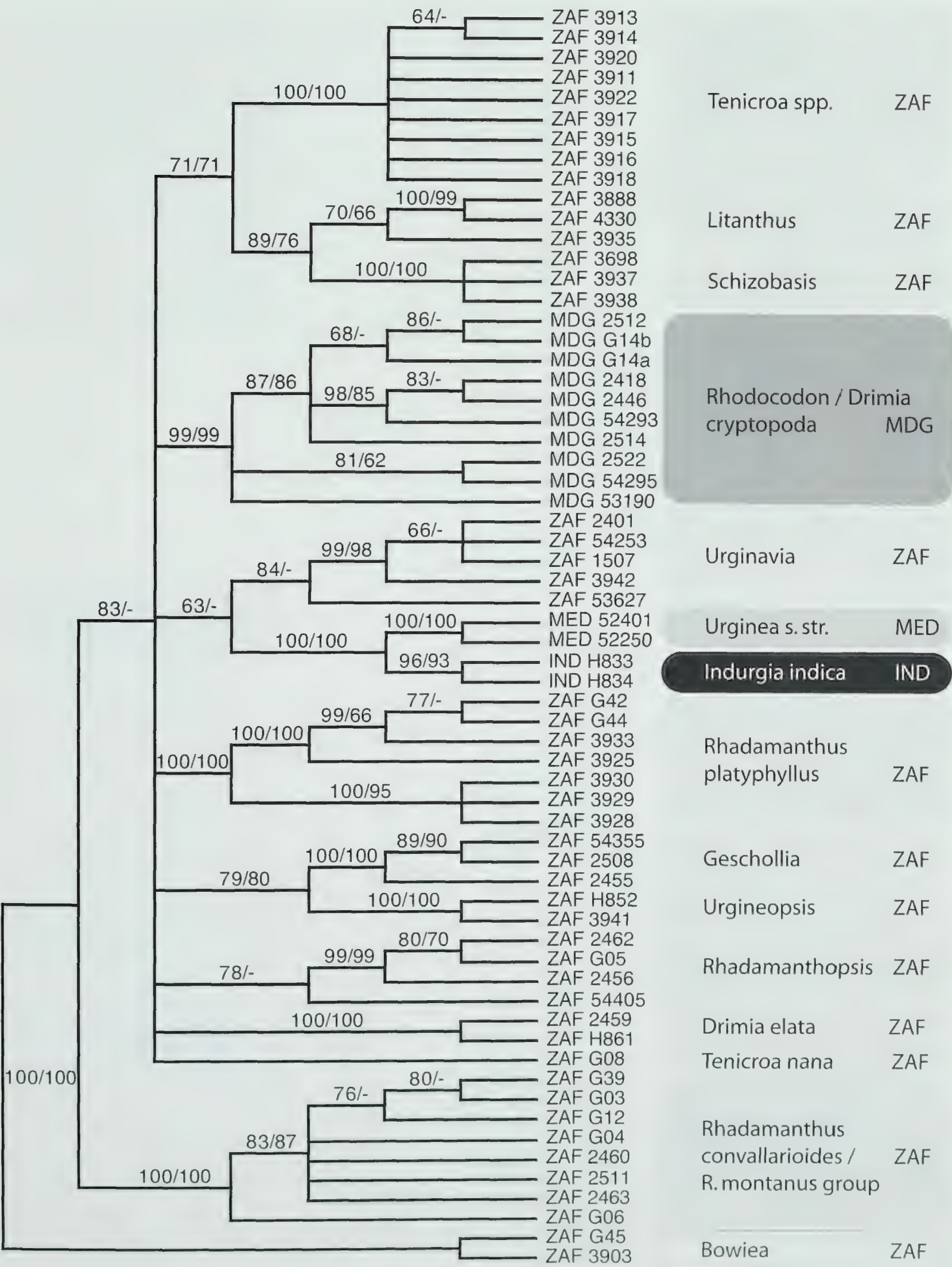


Figure 1 – Phylogenetic reconstruction based on maximum parsimony of members of subfamily Urgineoideae. A strict consensus tree is shown with bootstrap support values (including/excluding indel data) indicated above branches. Major clades are colour-coded by geographic affiliations (light grey shading – South Africa [ZAF], dark grey shading – Madagascar [MDG], black – India [IND], medium grey shading Mediterranean [MED]; outgroup: *Bowiea* from South Africa [ZAF] – no shading, black frame)

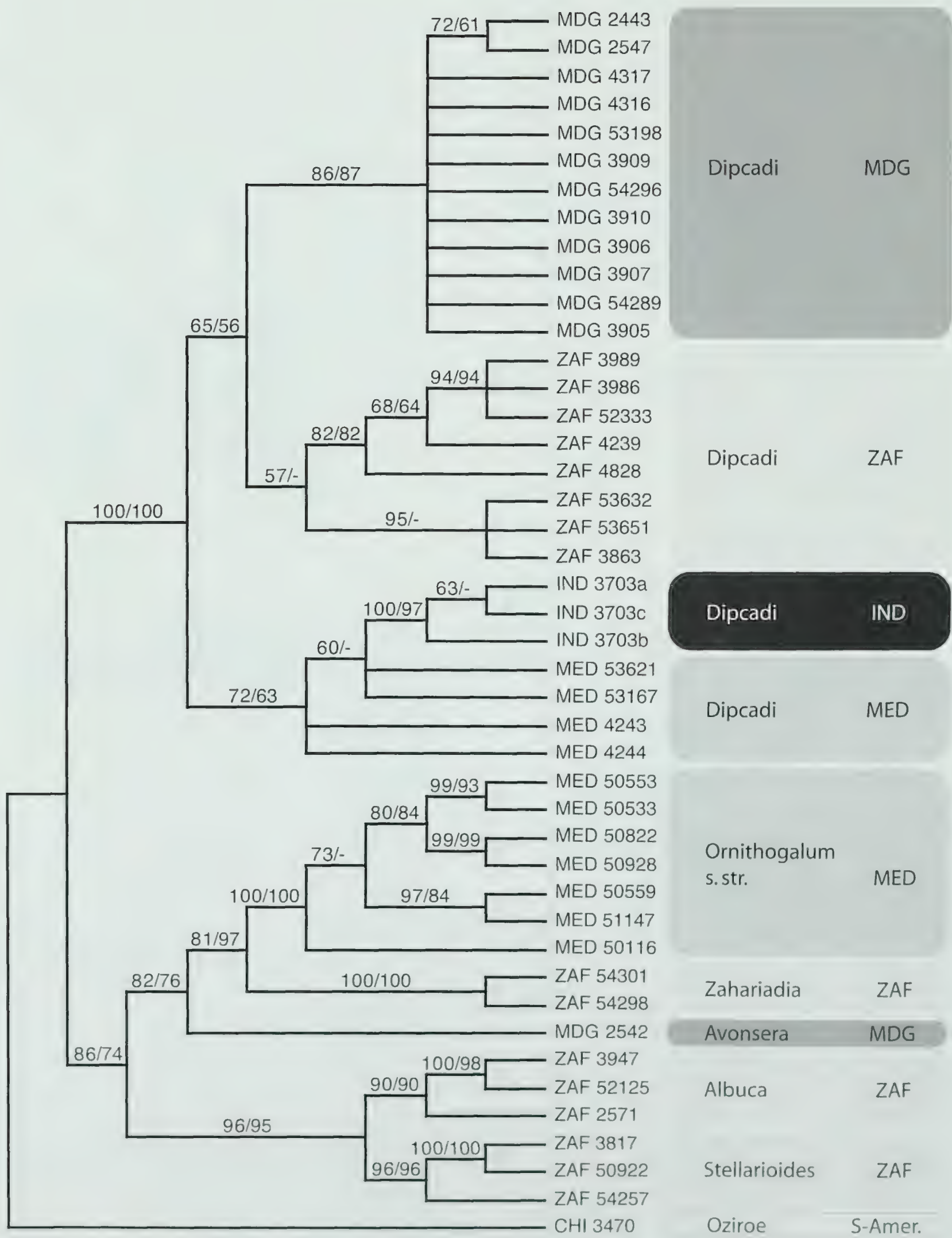


Figure 2 – Phylogenetic reconstruction based on maximum parsimony of members of subfamily Ornithogaloideae using *Ozirooe* from South American subfamily Ozirocoideae as outgroup. A strict consensus tree is shown with bootstrap support values (including/excluding indel data) indicated above branches. Major clades are colour-coded by geographic affiliations (light grey shading – South Africa [ZAF], dark grey shading – Madagascar [MDG], black – India [IND], medium grey shading – Mediterranean [MED]; outgroup: *Ozirooe* from South America [S-Amer.] – no shading, black frame)

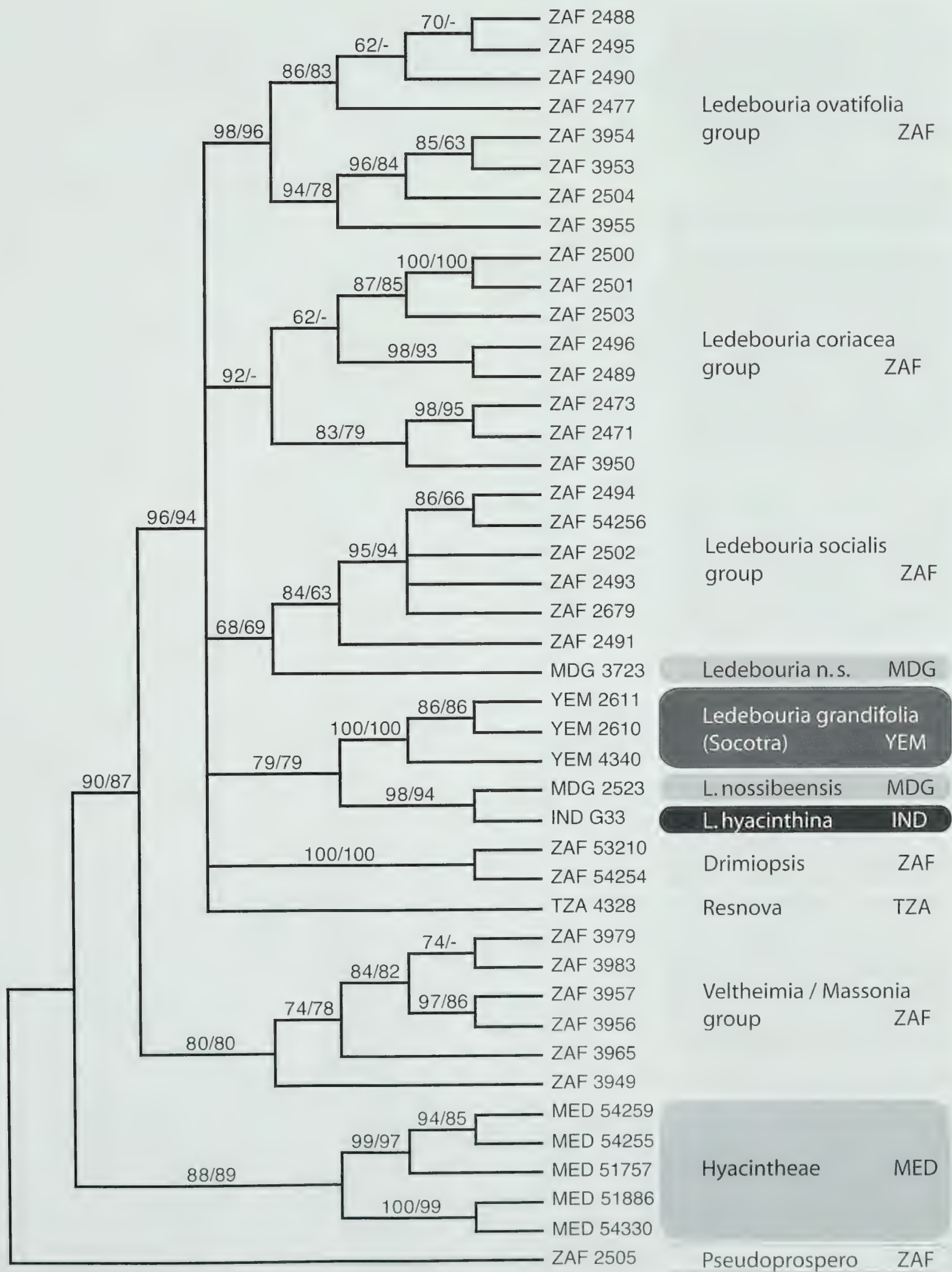


Figure 3 – Phylogenetic reconstruction based on maximum parsimony of members of subfamily Hyacinthoideae. A strict consensus tree is shown with bootstrap support values (including/excluding indel data) indicated above branches. Major clades are colour-coded by geographic affiliations (light grey shading – South Africa [ZAF] and Tanzania [TZA], dark grey shading/black text – Madagascar [MDG], dark grey shading/white text – Arabian Peninsula [Yemen - YEM], black – India [IND], medium grey shading – Mediterranean [MED]; outgroup: *Pseudoprospero* from South Africa [ZAF] – no shading, black frame).

and Hyacinthoideae, respectively. Subfamily Ornithogaloideae was rooted with Oziroeoideae, the most basal subfamily in Hyacinthaceae. Topological findings in subfamilies Urgineoideae, Ornithogaloideae, and Hyacinthoideae, directly address the origin and diversification of Hyacinthaceae in Madagascar and India.

Subfamily Urgineoideae

All species from Madagascar form a clade (fig. 1). This clade (99/99% +indels/-indels bootstrap support) includes all species of *Rhodocodon* as well as the frequently misclassified and morphologically deviant *Drimia cryptopoda*. Originally, the latter species was included in *Hyacinthus* (subfamily Hyacinthoideae), yet it was shown to belong to Urgineoideae instead (Pfosser et al. 2006, Wetschnig et al. 2007). Our results suggest that *D. cryptopoda* is closely related to other Malagasy members of Urgineoideae. The entire clade is nested within a group of predominantly South African species. The monophyly of this well-supported clade suggests a single colonization for the Malagasy alliance from continental Africa. Inclusion of the Malagasy taxa in *Rhadamanthus* as suggested by Pfosser & Speta (2004) is clearly refuted by this topology. The Indian taxa form a well-supported clade (100/100%) with the Mediterranean *Urginea* Steinh. s. str, indicating a Northern Hemisphere diversification after migration of progenitors of this group from South Africa.

Subfamily Ornithogaloideae

Within Ornithogaloideae only *Dipcadi* is found in all of South Africa, Madagascar, India and the Mediterranean. The genus is well supported (100/100%). As in *Rhodocodon*, the Malagasy members of *Dipcadi* show a pattern suggesting a single colonization from mainland Africa followed by rapid radiation and speciation in Madagascar. The Malagasy species form a well-supported clade (86/87% bootstrap support). Although a direct relationship to South African *Dipcadi* is only moderately supported (65/56% bootstrap support), a direct relationship to Indian *Dipcadi* has to be dismissed. Again, an affinity of the Indian taxa to the Mediterranean species is suggested (72/63% bootstrap support). Possible migration routes linking the Mediterranean and India (perhaps via the Arabian Peninsula where this genus is also present) are pending further investigation.

Subfamily Hyacinthoideae

Two species of *Ledebouria* are known from Madagascar. *L. nossibeensis* shows strong relationships to the type species of *Ledebouria*, *L. hyacinthina* from India (98/94% bootstrap support). Sister group relationship of this clade with *Ledebouria grandifolia* from Socotra receives moderate support (79/78% bootstrap support). A second unrelated *Ledebouria* species is found in the south-western parts of Madagascar and remains to be described. This species shows moderate affinity to the *L. socialis*-group of continental Africa (68/69% bootstrap support). In *Ledebouria* therefore, two colonization events must be envisaged to explain the present distribution of the genus in Madagascar. No direct relatives to either the Malagasy, Arabian or Indian members of the

genus are found in the Mediterranean, hence excluding the possibility of Northern Hemisphere migration routes having played a role in the diversification of this group. In contrast, the tree topology reflects the most recent tribal classification into strictly Northern Hemisphere (excluding India) Hyacintheae (88/89%), the monotypic South African tribe Pseudoprosperae (genus *Pseudoprospero*) and tribe Massonieae (87/82%) including all remaining African and all Indian and Malagasy species in this subfamily (Manning et al. 2004). Moreover, our data again show the need to revise generic classification within a broadly defined *Ledebouria*. Obviously, in this group phylogenetically unrelated lineages are present, which also show distinct geographic radiation patterns that could warrant further splitting into separate genera as already suggested by Lebatha et al. (2006).

Both *Dipcadi* and *Rhodocodon* (including *Drimia cryptopoda*) are genera with numerous species on Madagascar and show well-supported monophyletic groups for the Malagasy alliances in the phylogenetic reconstructions. This points to single colonization events followed by subsequent radiation on the island. In both cases the island taxa appear to be descendants of dispersers of African origin. Similar scenarios have been evoked for most of the present-day biota of Madagascar (Yoder & Nowak 2006). As both the Urgineoideae and Ornithogaloideae trees do not suggest a direct relationship of these Malagasy groups to members in India, a Gondwana origin leading to vicariance after continental break-up as previously suggested appears to be less likely (Pfosser & Speta 1999). A Gondwana origin as an explanation for the present day distribution of Hyacinthaceae would require an age of the radiations in Madagascar and India similar to the fragmentation of Gondwana in the Cretaceous.

Ledebouria is the only example in Hyacinthaceae where direct relatives are found in Africa, Madagascar, Arabian Peninsula, and India. *Ledebouria* therefore resembles a distribution pattern found also in other groups, where a Gondwana origin was postulated (Conti et al. 2004, Rutschmann et al. 2004, Ashton & Gunatilleke 1987, Ducousso et al. 2004). However, the age of Hyacinthaceae was determined to be less than 40 Myr (Wikström et al. 2001), much younger than the breakup of Gondwana (120–80 Myr ago). A major drawback in dating radiations in Hyacinthaceae is the lack of fossil data. Recently, the arrival of progenitors of the *Rhodocodon/Drimia cryptopoda*-clade in Madagascar was dated by a molecular clock-approach at 5–15 Myr ago (Ali et al. 2011). Interestingly, prevalence of oceanic currents directed eastward from Mozambique towards Madagascar have recently been found based on palaeogeographic reconstruction during the Paleogene (c. 60–20 Myr ago), exactly as required for the establishment of many of the unique floristic and faunistic elements of Madagascar (Ali & Huber 2010) and much closer to the dated arrival of Urgineoideae in Madagascar. According to their hypothesis, rafting (e.g. on large vegetation mats) might have been a common vehicle for progenitors to arrive on Madagascar during this period.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com>).

com/content/botbel/plecevo/supp-data), and consist of a list of taxa investigated in this study, with vouchers, and EMBL accession numbers (pdf format.)

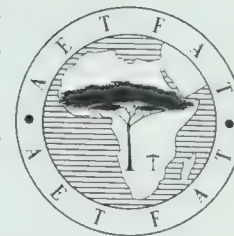
ACKNOWLEDGEMENTS

We are grateful to Jacky Andriantiana (Madagascar) and Anton Sieder (Vienna, Austria) who helped in collecting material in Madagascar for this analysis. The useful comments of Laco Mucina and Magnus Lidén during the reviewing process are gratefully acknowledged.

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- Manuscript received 31 Oct. 2010; accepted in revised version 25 Oct. 2011. This paper was pre-published on 12 Mar. 2012 in issue 145(1) of *Plant Ecology and Evolution*.
- Communicating Editor: Mats Thulin.



Jumellea pailleri (Orchidaceae), une espèce nouvelle endémique des Comores

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Jumellea pailleri (Orchidaceae), a new endemic species from Comoro Archipelago

Background and aims – *Jumellea pailleri* F.Rakotoar. (Orchidaceae), a new endemic species from the Comoro Archipelago is described and illustrated.

Methods – Description and comparison of herbarium material from the herbarium of Comoro and Réunion Islands University (REU) have been done.

Key results – Different from other *Jumellea* species from Comoro Island, *J. pailleri* resembles to *J. bathiei* Schltr. and *J. ibityana* Schltr., which are endemic to Madagascar. A key to identify *Jumellea* species from Comoro Islands is provided. The new species is illustrated, its distribution is given and its conservation status.

Key words – Orchidaceae, *Jumellea*, *J. bathiei*, *J. ibityana*, *J. pailleri*, taxonomy, Indian Ocean, Grand Comoro, Comoro Archipelago.

Contexte et but visé – *Jumellea pailleri* F.Rakotoar. (Orchidaceae), une espèce nouvelle endémique des Comores est décrite et illustrée.

Méthodes – Une description et une comparaison avec les spécimens d'herbiers de *Jumellea* déposés aux Herbiers Universitaires des Comores et de La Réunion (REU) ont été effectuées.

Résultat-clés – Différente de toutes les autres espèces de *Jumellea*, *Jumellea pailleri* est proche de *J. bathiei* Schltr. et *J. ibityana* Schltr. qui sont endémiques de Madagascar. Une clé d'identification des espèces comoriennes est donnée, ainsi que les caractéristiques morphologiques, la distribution de la nouvelle espèce et son statut de conservation.

INTRODUCTION

De récentes études phylogénétiques sur les Angraecoïdes des Mascareignes (Micheneau et al. 2008) ont révélé que le genre *Jumellea* Schltr. forme un groupe monophylétique principalement présent à Madagascar mais aussi dans les îles océaniques avoisinantes telles que les îles des Comores et des Mascareignes, et allant jusqu'en Afrique de l'Est (Wood 1982, La Croix 2000). En tout, le genre compte 58 espèces dont deux en Afrique de l'Est, cinq aux Comores, 42 à Madagascar et neuf aux Mascareignes (Perrier de la Bâthie 1939, Du Puy et al. 1999, Stewart et al. 2006). Récemment, Cribb & Hermans (2009) dans leur guide des Orchidées malgaches ont recensé 41 espèces à Madagascar, Comores et Mascareignes, et deux espèces en Afrique tropicale. Pailler et al. (2008) ont aussi

signalé la présence de deux espèces malgaches aux Comores, il s'agit de *J. confusa* Schltr. et *J. maxillarioides* Schltr.

Décrit pour la première fois en 1914 par Rudolf Schlechter, le genre *Jumellea* se distingue clairement des genres voisins *Angraecum* Bory et *Aeranthes* Lindl. par ses inflorescences uniflores, ses fleurs toujours de couleur blanche et ses fruits fusiformes. *Jumellea* est caractérisé par ses fleurs à structure très uniforme (La Croix 2000): sépales latéraux soudés à la base, se projetant vers l'avant avec les pétales et le labelle; labelle entier, toujours contracté à la base, creusé en gouttière, reliée à l'orifice de l'éperon; et colonne dilatée à la base, prolongée en deux bras parallèles soudés aux bords de l'orifice de l'éperon du côté interne et aux sépales et pétales du côté externe.

Peu d'études ont été menées sur la taxonomie du genre. Depuis la dernière révision complète de Perrier de la Bâthie

Clé d'identification des *Jumellea* présentes aux Comores

1.	Plantes subacaules.....	2
1'.	Plantes caulescentes.....	5
2.	Feuilles de plus de 40 cm de longueur.....	3
2'.	Feuilles de moins de 40 cm de longueur.....	4
3.	Ovaire pédicellé, égalant $\pm$ le pédoncule.....	<i>J. arachnantha</i>
3'.	Ovaire pédicellé plus court que le pédoncule.....	<i>J. gladiator</i>
4.	Eperon de moins de 5 cm de longueur.....	<i>J. phalaenophora</i>
4'.	Eperon de plus de 5 cm de longueur.....	<i>J. maxillarioides</i>
5.	Feuilles de moins de 9 cm de longueur.....	6
5'.	Feuilles de plus de 9 cm de longueur.....	<i>J. confusa</i>
6.	Pédoncule de moins de 10 mm de longueur.....	<i>J. anjouanensis</i>
6'.	Pédoncule de plus de 10 mm de longueur.....	7
7.	Eperon de moins de 10 cm de longueur.....	<i>J. pailleri</i>
7'.	Eperon de plus de 10 cm de longueur.....	<i>J. comorensis</i>

(1939), huit nouvelles espèces de *Jumellea* ont été légitimement décrites (Summerhayes 1952, Senghas 1964, Senghas 1967, Bosser 1970, Wood 1982, La Croix 2000, Cribb 2009, Pailler 2009). Les espèces de *Jumella* se distinguent par la longueur de l'éperon, la taille de la fleur, la présence ou absence de la tige, et la forme et la taille des feuilles. Dans le cadre de notre révision taxonomique en cours, une nouvelle espèce a été récemment découverte dans l'île de la Grande Comore (Ngazidja), que nous décrivons ici. Cette nouvelle espèce ne ressemble à aucune autre espèce décrite au sein du genre. *Jumellea pailleri* se caractérise par la présence d'apicules au sommet des pièces florales et a été localisée sur des crêtes de haute et moyenne altitudes où la végétation est de type humide à canopée très ouverte.

METHODOLOGIE

Les caractéristiques de *Jumellea pailleri* ont été observées et mesurées à partir des herbiers secs sauf pour les fleurs qui ont été conservées dans de l'alcool à 70° avant mesures. Les échantillons de cette nouvelle espèce ont été comparés avec ceux des autres espèces de *Jumellea* disponibles dans les Herbiers de REU, TAN et P afin de confirmer son statut de nouvelle espèce, de déterminer les espèces les plus proches morphologiquement et de noter ses caractéristiques propres.

RÉSULTATS

Jumellea pailleri F.Rakotoar., *Pl. Ecol. Evol.* 144:364 (2011). Affinis *J. bathiei* Schltr. atque *J. ibityanae* Schltr. statura, calcaris longitudine formaque affinis sed ambabus, aeriis radicibus percurrentibus super efoliatae caulae totam longitudinem et foliorum inferiore parte valde eminentibus nervis (apud *J. bathiei* et *J. ibityanae* aeriis radicibus caulae solum basi atque foliorum inferiore parte subleve), longioribus inflorescentiis, perianthii partibus minoribus apiculatisque (apud *J. bathiei* et *J. ibityanae*, perianthium partibus media statura muticisque) praecipue differt. – Type: Grande Comore, La Grille, 11°27'S 43°20'E, alt. 1076 m, 27 Fév. 2009, *Rakotoarivelo* 60 (holo-: REU; iso-: REU, COM, TAN, P).

Plante épiphyte à tige rigide, ramifiée, à section cylindrique (4–5 mm) pouvant atteindre 40 cm de longueur, portant des feuilles (3–7) dans le tiers supérieur. Racines aériennes réparties sur toute la partie défeuillée de la tige et perçant les gaines foliaires (13–20 mm), persistantes et opposées aux fleurs des années précédentes. Feuilles (6–9 × 1,2–1,5 cm) coriaces, rigides, planes, non odorantes, elliptiques, inégalement bilobées à l'apex avec une échancrure profonde, à face inférieure présentant une à nervure sail-lante en séchant. Inflorescences latérales, perçant les gaines foliaires, sub-pérénnes, produisant une fleur à la fois durant deux années consécutives. Pédoncule court (1,2–3,5 cm), portant 4 gaines persistantes, imbriquées dont la quatrième située vers la moitié. Bractée tubuliforme (6–8 mm), persis-tante et obtuse, de forme et taille identique à la plus grande gaine du pédoncule. Ovaire pédicellé, deux fois plus long que le pédoncule (5–6 cm). Fleur blanche, caractérisée par des sépales et pétales festonnés à la base. Sépale adaxial (12–14 × 1,5–2 mm) droit, oblong, rugueux dessous, apiculé. Sépales latéraux légèrement arqués, de même taille et forme que le sépale adaxial. Pétales oblongs, légèrement plus longs que les sépales (13–15 × 1,5–2 mm), apiculés. Labelle ovale (14–16,5 mm × 5–6 mm), naviculaire, rétréci à la base, élargi au deux tiers, non anguleux, muni d'une carénule médiane attein-gnant le centre (7 mm), apiculé. Éperon filiforme courbé à la base, $\pm$ 41 mm de longueur, plus long que le labelle mais plus court que l'ovaire pédicellé. Colonne de 3 mm de hauteur sur 2–3 mm de largeur. Anthère munie d'une carénule médiane recouvrant les deux auricules au niveau de la partie conni-vente. Dent très petite et aiguë au fond de l'échancrure du rostelle. Auricules conniventes, anguleuses aux extrémités, se projetant vers l'avant. Fruit: capsule fusiforme conforme aux autres espèces du genre, longue de $\pm$ 4 cm. Fig. 1.

Spécimens examinés – Grande Comore: La Grille, 11°27'S 43°20'E, alt. 1076 m, Fév. 2009, *Rakotoarivelo* 59 (REU); Ibid., Fév. 2009, *Rakotoarivelo* 60, (REU); Ibid., Mar. 2010, *Blambert H.B.* 71 (REU); Karthala, 11°45'S 43°20'E, alt. 2100 m, Juil. 2008, *Boulongne* 64 (K).

Distribution – Espèce endémique de La Grande Comore, *Jumellea pailleri* a une distribution très restreinte, elle est uniquement rencontrée sur les crêtes du massif de La Grille à



Figure 1 – *Jumellea pailleri*: A, port de la plante; B, fleur de profil; C, sépales (s), pétales (p) et labelle (l); D, colonne vue de 3/4; E, colonne vue de dessous; F, pollinie; G, clinandre. Réalisée par William Andriananjavelo.

une altitude d'environ 1000 m et sur le flanc ouest du massif du Karthala à 2100 m.

Ecologie – *Jumellea pailleri* pousse en épiphyte sur les troncs d'arbres à l'ombre ou sur les branches exposées au soleil. Elle se rencontre dans les forêts humides de moyenne altitude (1000 m) à voûte plus ou moins fermée ainsi que dans les fourrés éricoïdes de hautes altitudes. Les deux massifs qui abritent l'espèce sont des massifs volcaniques à sol très mince et basaltique.

Affinités – *Jumellea pailleri* F.Rakotoar. se différencie nettement des autres espèces de *Jumellea* qui sont recensées aux Comores. C'est la seule espèce comorienne à tige qui a un court éperon mesurant ± 41 mm. Après comparaison des planches d'herbiers (COM, K, P, REU, TAN), *Jumellea pailleri* n'est ni présente en Afrique de l'Est, ni à Madagascar, ni aux Mascareignes. Elle est proche de *J. bathiei* Schltr. et *J.*

ibityana Schltr. par sa taille, par la longueur et la forme de son éperon. *J. pailleri* se distingue de ces deux espèces par ses racines aériennes réparties le long de la tige et par ses feuilles à nervures saillantes sur la face inférieure alors que chez *J. bathiei* et *J. ibityana*, les racines aériennes ne sont présentes qu'à la base des tiges et les feuilles sont plus ou moins lisses à la face inférieure. Les inflorescences sont plus longues chez *J. pailleri* (7,5–12 cm) alors qu'elles sont courtes chez *J. bathiei* et *J. ibityana* (5–7 cm); les pièces du périanthe sont de petite taille ($12\text{--}14 \times 1,5\text{--}2$ mm) et apiculées à l'apex, alors qu'elles sont de taille moyenne ($17\text{--}21 \times 3\text{--}7$ mm) et mutiques chez *J. bathiei* et *J. ibityana*. Enfin des analyses phylogénétiques en cours (Rakotoarivelo & Paillet, données non publiées), montrent que l'espèce n'est pas du tout apparentée aux espèces desquelles elle se rapproche morphologiquement (*J. bathiei* et *J. ibityana*). Ceci nous permet de confirmer que l'espèce est bien nouvelle.

Conservation – Parmi les trois îles des Comores (Grande Comore, Mohéli, et Mayotte) où nous avons effectué nos collectes de données, *Jumellea pailleri* n'est présent qu'à la Grande Comore. Elle a été collectée pour la première fois, en 2008, par Boulongne (K, !) et jusqu'à présent aucun document n'a signalé sa présence ailleurs. Les massifs de La Grille et de Karthala abritent la majorité des espèces endémiques Comoriennes (plus de 50% pour la famille des orchidées, avec 45 espèces endémiques). Cependant, ils ne font l'objet d'aucune mesure de protection. Des propositions de délimitation et de zonage d'une aire protégée au niveau de la forêt du Karthala ont déjà été mentionnées dans des études (Abdulhamide 2005, Colloque international sur le Karthala 2008), mais n'ont pas encore été mis en place. De ces faits les activités humaines sont permanentes et la régression des habitats où pousse *Jumellea pailleri* constitue une menace pour la survie des populations de cette espèce.

Nos investigations de terrain ont montré que le nombre d'individus matures de *Jumellea pailleri* dans la nature ne dépasse pas cinquante. De plus, les zones d'occurrence et d'occupation sont très restreintes. Par conséquent, nous attribuons à *J. pailleri* le statut de conservation "CR D" selon l'UICN (2001).

Étymologie – La plante est dédiée à Thierry Pailler, enseignant-chercheur à l'Université de La Réunion conduisant des recherches sur les Orchidaceae du sud-ouest de l'Océan Indien. Thierry Pailler a été le premier à repérer l'espèce dans son habitat naturel lors de notre expédition aux Comores en Février 2009.

GLOSSAIRE

Apiculé – Organe terminé brusquement par une courte pointe relativement large et peu aiguë.

Aigu, aiguë – Qui se rétrécit progressivement en pointe.

Carénule – Saillie longitudinale à section triangulaire ou à angle marqué que présente le dos ou la surface de certains organes.

Ovaire pédicellé – Chez les *Jumellea* la fleur est portée par un long pédicelle (tige qui porte la fleur solitaire) relié directement à l'ovaire infère.

REMERCIEMENTS

Les auteurs remercient Jacques Florence et Daniel Geerinck pour la diagnose latine, les relecteurs anonymes pour leurs remarques constructives et éclairantes et, William Andriananjavelo pour les dessins. Fanny Rakotoarivelo est bénéficiaire d'une Bourse de Coopération régionale de la Région Réunion et Thierry Pailler est bénéficiaire d'un projet de recherche financé par National Geographic Society (Systematics and evolution of the *Jumellea* genus (Orchidaceae) in the West Indian Ocean (Madagascar, Mascarenes, Comoros), Grant number #8611-09).

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Manuscript received 5 Aug. 2010; accepted in revised version 30 Jun. 2011. This paper was pre-published on 15 Nov. 2011 in issue 144(3) of *Plant Ecology and Evolution*.

Communicating Editor: Tariq Stévant.



Trianthema subg. *Papularia* (Aizoaceae) in Africa

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Background and aims – Following a comprehensive study in the genus *Trianthema* (Aizoaceae – Sesuvioideae), in which the subdivision into two subgenera was confirmed and analysed in detail (Hartmann et al. 2011), including new clear delimitations of 17 species worldwide in *T.* subg. *Papularia*, a survey of the African species is presented here.

Methods – Normal practices of herbarium taxonomy have been applied to study all herbarium material available, mainly from B, C, E, HBG, K, L, MO, UTB, WAG, and Z.

Key results – Of the seventeen species in *T.* subg. *Papularia*, twelve are found in Africa: *T. corallicola*, *T. corymbosa*, *T. crystallina*, *T. hereroensis*, *T. mozambiquensis*, *T. parvifolia*, *T. salsoloides*, *T. sanguinea*, *T. sedifolia*, *T. sheilae*, *T. transvaalensis* and *T. vleiensis*. Morphological investigations were undertaken as widely as the available material permitted, resulting in distinct character set per species, showing also that the area of each species is much smaller than hitherto anticipated and used in flora treatments.

Key words – Aizoaceae, comparative morphology, *Cypselea*, distribution of species, *Papularia*, *Sesuvium*, Sesuvioideae, taxonomy, *Trianthema*, *Tribulocarpus*, *Zaleya*.

INTRODUCTION

When studies in the subfamily Sesuvioideae (Aizoaceae) in Africa were intensified by the inclusion of DNA analyses (Hassan et al. 2005b), it was soon found that due to neglectance over decades, the circumscription of the two subgenera as well as of species in the genus *Trianthema* required a consideration of all taxa worldwide. Not only had names been confused since about 200 years, but the identification of species was arbitrary, as demonstrated by the fact that figures of African material were used for illustration in floras in other parts of the world. Furthermore, the subdivision into the two subgenera *Trianthema* subg. *Trianthema* and *Trianthema* subg. *Papularia* (Jeffrey 1960) had neither been studied since they had been established nor had it been applied in the sense that more than the type species were assigned to the subgenera.

Results from a comprehensive study by Hartmann et al. (2011) reveal that:

- (1) the subdivision of the subgenera is confirmed,
- (2) seventeen species can be distinguished in *Trianthema* subg. *Papularia*: *T. corallicola*, *T. mozambiquensis*, *T. pakistanensis*, *T. ufoensis*, and *T. vleiensis* as new; *T. clavata* and *T. corymbosa* have been raised to species rank, and *T. crystallina*, *T. hereroensis*, *T. parvifolia*, *T. salsoloides*, *T. sanguinea*, *T. sedifolia*, *T. sheilae*, *T. trans-*

vaalensis, as well as *T. triquetra* have been emended and re-circumscribed. Only *T. argentina* remains unaltered.

- (3) in contrast to older species name applications, it was found that not a single species in the subgenus occurs in a wider area covering more than one continent, implying that the formerly assumed extensive distribution of certain species was a consequence of wrong taxonomic conclusions. Instead, areas of species are limited, and twelve are recognized in and restricted to Africa, most of them growing allopatrically. Included are, however, collections from the southwest of the Arabian Peninsula because the restricted documented distribution area of *T. crystallina* may be a result of undercollecting due to the widespread belief that the species was common (Collenette, pers. comm) and hence no fresh collections were made.

This paper relies on the morphological data presented in Hartmann et al. (2011) with appropriate illustrations; only those features are mentioned here that have a bearing on the African material.

MATERIAL AND METHODS

Four hundred and fifty collections of *Trianthema* formed the base of the original investigations on a worldwide base, 83 of these made by H.E.K.H. in Kenya, Namibia, South Africa, Sudan, Tanzania, United Arab Emirates, and Zimbabwe, the

bulk having been made available by loan from the herbaria AD, B, BRI, C, DNA, E, HBG, K, L, MO, UTB, WAG, and Z, including type sheets. All specimens cited were seen, unless otherwise indicated ('n.v.').

Morphological studies were expanded to cover almost all characters from dry herbarium material and material preserved in liquid, from observations made in habitat, freshly sent plants from South America, and from numerous images. Beside investigations with a binocular microscope, SEM graphs of surfaces were prepared and studied in a Philips/FEI XL 30 ESEM at Bayreuth by U. Meve.

The chorology of the taxa is interpreted in terms of the chorological division of Africa proposed by White (1983, 1993), modified by Jürgens (1991) and Clarke (1991) and applied to Southwest Asia (White & Léonard 1991).

RESULTS OF MORPHOLOGICAL STUDIES

Life span and related features

Two features occur in African material only, deviating from the usual perennial life form:

- some species can flower in their first year of growth already, e.g. observed in *T. corallicola*, *T. parvifolia*, *T. salsoloides*, *T. sheilae*, and *T. transvaalensis*, but in favourable conditions they will continue to grow over few (*T. transvaalensis*) to many years (*T. sheilae*). Such changes cannot be detected in herbarium material, nor can notes on the subject be found easily. More species may follow this pattern, but data from the wild are scarce;
- decumbent growth can be seen in annual plants regularly, but only adult plants of several years permit a clear recognition of erect growth, e.g. in *T. corymbosa*, against persisting decumbent growth, as, e.g., in *T. parvifolia*. Notable is, however, that populations of *T. parvifolia* in the north tend to develop oblique to erect branches.

Remarkable is also that shedding of leaves seems to be restricted to plants of *T. corymbosa* (described originally as a variety of *T. crystallina* by Sonder in 1862).

The species that grow strictly as annuals in Africa are probably *T. sanguinea* and *T. sedifolia*, as far as information is available at this date.

Internodes

When assessing the equipment of bladder cells on the internodes, it must be considered that the number of bladder cells is determined early in the ontogeny. During elongation and growth, the normal epidermal cells increase in numbers, but not the bladder cells. In consequence, young internodes will always appear rougher from more bladder cells on a fixed surface area, and older internodes will look more sparsely ornamented.

Predominantly smooth internodes have been reported for *T. corymbosa* (fig. 4A in Hartmann et al. 2011) and *T. hereroensis* (fig. 10A in Hartmann et al. 2011), and *T. parvifolia*, but populations in the north exhibit bladder cells as well.

Globose bladder cells (size at most up to 100 µm) have been found in *T. mozambiquensis* (fig. 11A in Hartmann et

al. 2011), *T. salsoloides* (fig. 6A in Hartmann et al. 2011), *T. sanguinea* (fig. 7A in Hartmann et al. 2011), and *T. vleiensis* (fig. 9F in Hartmann et al. 2011), all in loose arrangement on the surface. Bigger (about 150–170 µm) and more densely placed bladder cells on internodes have been documented for *T. crystallina* (fig. 2B in Hartmann et al. 2011), *T. sedifolia* (fig. 7E in Hartmann et al. 2011), and *T. sheilae* (fig. 1E in Hartmann et al. 2011). Also densely placed but of an elongate ovoid shape are the bladder cells on internodes in *T. transvaalensis* (fig. 6E in Hartmann et al. 2011). Prominent elongated bladder cells to 500 µm long adorn the internodes of *T. corallicola* (fig. 8A in Hartmann et al. 2011) in a rather dense arrangement, a unique feature in the genus.

Internode length depends largely on growing conditions and on the state the individual is in when assessed; measurements of internodes are, therefore, not of value in distinguishing species.

Leaves

General features – Like all members of the subfamily Sesuvioideae, leaves of *Trianthema* consist of three parts: the leaf blade, a petiole, and two flaps at each side of the petiole, called often stipules, although they are not formed early in ontogeny, as would be the case in true stipules; instead, these flaps are also called pseudo-stipules here.

Shapes of leaf blades – Although the dried leaves of *Trianthema* appear flat in herbarium specimens, they start off as vigorous succulent three dimensional organs. Fresh leaves are rarely present for assessment, but it seems that most species form succulent leaves often a little wider than thick, and in some cases the margins are even rolled in the dry state, e.g. in *T. mozambiquensis* (fig. 11B in Hartmann et al. 2011) and *T. sanguinea* (fig. 7B in Hartmann et al. 2011).

Constant are, however, differences in the formation of the leaf tip:

- rounded leaf tips are found in *T. corymbosa* (fig. 4A), *T. crystallina* (fig. 2C), *T. parvifolia* (fig. 4E), *T. sedifolia* (fig. 7F), and *T. sheilae*, all figured in Hartmann et al. 2011;
- prominent are the sharp tips of *T. corallicola* (fig. 8E in Hartmann et al. 2011), in which species the tips are adorned with prominent papillae resulting in a fuzzy look of the tip. Acute leaf tips are also found in *T. hereroensis* (fig. 10C in Hartmann et al. 2011), distinguishing it at first sight from *T. parvifolia*, with which it has been united in the past.

Also equipped with apical papillae are the leaves of *T. transvaalensis* in their young state, but less prominent and not as long as those of *T. corallicola*.

More acuminate than acute the leaf tips of *T. salsoloides*, *T. sanguinea*, and *T. vleiensis* (fig. 9C & E in Hartmann et al. 2011) present themselves.

Leaves on the only collection of *T. mozambiquensis* are rolled up so narrowly that they appear acuminate pointed, but fresh material will be needed to assess the leaf shape definitely.

Since the leaf tips are the first parts of a leaf to develop in ontogeny, their shape and sculpture can be understood to rep-

resent old genetically determined lines, less variable under changing environmental conditions, as has been checked in larger samples in detail.

Leaf blade surfaces – Like internodes, leaf blades differ in their equipment with bladder cells. Almost smooth blades with only slightly raised bladder cells are known from *T. corymbosa*, *T. hereroensis*, and *T. parvifolia* (fig. 4E in Hartmann et al. 2011), all three also without bladder cells on their internodes; and in *T. vleiensis* (fig. 9C in Hartmann et al. 2011), small bladder cells of about 100 µm are also encountered on their internodes. Covered by big yet very low bladder cells are the leaf blades of *T. mozambiquensis* (fig. 11B in Hartmann et al. 2011), here in combination with prominent bladder cells on the internodes (fig. 11A in Hartmann et al. 2011). Few to some large globose bladder cells of about 200 µm can be seen distributed all over the blade in *T. sedifolia* (fig. 7F in Hartmann et al. 2011); pointed bladder cells of ca 160 µm sit mainly along the margins in *T. transvaalensis*; very prominent bladder cells almost forming hairs adorn the tip of the blade in *T. corallicola* (fig. 8E in Hartmann et al. 2011), often visible to the naked eye. The most striking cover of big bladder cells occurs in blades of *T. crystallina* (fig. 2C in Hartmann et al. 2011) and *T. sheilae* (fig. 1F in Hartmann et al. 2011), in this way forming a complete secondary cover over the normal epidermis by densely placed globose bladder cells of 150–230 µm diam.

Colour patterns on the upper leaf surface – Bittrich (1990) pointed out already that a dark or green line can be seen in fresh leaves of some members of the genus *Trianthema* based on studies in Australian material. Field observations in southern Africa permit the description of three different types of colour patterns:

1. A longitudinal line above the mid vein of the leaf is conspicuous on the upper leaf surface in *T. transvaalensis* and *T. vleiensis* (fig. 9E in Hartmann et al. 2011), visible as a glassy stripe in translucent light, appearing dark green in reflecting light. In this area, the parenchymatic tissue reaches below the epidermis, no intermitting chlorenchymatous tissue being present. When drying, the leaf shrinks along this streak, which can be as long as or shorter than the upper leaf surface, sometimes recognizable as an inward fold on the dry leaf, difficult to distinguish under the binocular microscope (fig. 9C in Hartmann et al. 2011).
2. Local green dots can be seen in *T. parvifolia* (fig. 4D in Hartmann et al. 2011) and *T. corymbosa* (fig. 4A in Hartmann et al. 2011), very rarely aggregating in short sections along the upper surface above the mid vein, joining into something resembling short stripes, but always formed by more or less clearly separated dots.
3. Until now, no colour pattern has been found in all other species. This is certainly true for *T. crystallina* and *T. sheilae* with big bladder cells, but an assessment of the northern African populations and of *T. mozambiquensis* in the south an assessment is not possible at this date since no fresh material is available.

Petioles and lateral flaps – The most narrow pseudo-stipules (flaps) are present in *T. corymbosa* (fig. 4B in Hartmann et al. 2011), but in this species they merge into the petiole so

gradually that they seem to join the blade itself before the petiole could possibly separate from them.

Petioles of *T. vleiensis* (fig. 9B in Hartmann et al. 2011) are visible as well, the pseudo-stipules appearing like narrow flags to both sides and often ending in sharp little tips. *T. salsoloides* (fig. 6B in Hartmann et al. 2011) shows this type of pseudo-stipule as well, but in the otherwise very similar *T. transvaalensis*, the flaps are often less conspicuous (fig. 6E in Hartmann et al. 2011). Broad basal pseudo-stipules are also found in *T. mozambiquensis*, their shapes almost rectangular, ending in a short broad tooth of 90°, resulting in an almost flag-shaped appendage on either side of the petiole (fig. 11C in Hartmann et al. 2011), resembling *T. sedifolia* from Northern Africa most closely.

Most prominent are flaps in *T. crystallina* (fig. 2B in Hartmann et al. 2011) and *T. sheilae* (fig. 1F in Hartmann et al. 2011), in both cases very broad and ending in long-drawn acute points, 1–3 per pseudo-stipule, thus often appearing lacinate. Nevertheless, these flaps merge into the petiole, which in turn is sharply separated from the blade.

Very broad and more or less rectangular lateral flaps catch the eye in *T. parvifolia* (fig. 4E in Hartmann et al. 2011) and *T. corallicola* (fig. 8B in Hartmann et al. 2011). Especially in *T. parvifolia*, the pseudo-stipules remain regularly on the plant after the blades have withered and decayed, forming a prominent white papery envelope around the stem. Populations in the north of the distribution range tend to develop more narrow flaps, hence these plants have been named “*T. triquetra*” in the past.

T. hereroensis differs from all other species in the subgenus in having semi-elliptic pseudo-stipules (fig. 10C in Hartmann et al. 2011), the pair on a petiole forming a broadly elliptic shape.

Inflorescences – Rich axillary inflorescences arranged in close bundles are given as typical of the whole subgenus (Jeffrey 1960), and indeed can this feature be confirmed for most species. In young plants, the number of flowers can be only one, but usually other nodes will then show at least two flowers.

The flowers do not develop a pedicel, with the exception of *T. corymbosa*: in this species, the young flowers sit in close arrangement, elongating their pedicels while ripening, resulting in a long-drawn fruiting inflorescence by exposing the smooth pedicel surface.

A peduncle has not been found in members of the subgenus.

Differences exist, however, in the position of the flowers: usually they sit in a close bundle and are free. In *T. salsoloides* (fig. 6C in Hartmann et al. 2011) and *T. transvaalensis* (fig. 6F in Hartmann et al. 2011), however, tissue from the flower base surrounds the bases of the flowers resulting in a compact solid body that breaks out of the axil when old. This common feature has resulted in both species being considered to be one (e.g. Adamson 1962: 248, *T. salsoloides* var. *transvaalensis*), an arrangement not followed here (see also below under seeds).

Bracts and bracteoles – Each flower is subtended by a bract and, in most cases, by two bracteoles, differing in shape and size distinctly from the vegetative leaves.

Most common are lanceolate shapes in bracts and bracteoles, all usually placed at the bottom of the flower and free: *T. sanguinea* (fig. 7C in Hartmann et al. 2011), *T. sedifolia* (fig. 7G in Hartmann et al. 2011), *T. corallicola* (fig. 8A in Hartmann et al. 2011), *T. vleiensis* (fig. 9G in Hartmann et al. 2011), *T. hereroensis* (fig. 10B in Hartmann et al. 2011) are representative samples. Exceptions are found in *T. salsoloides* (fig. 6C in Hartmann et al. 2011) and *T. transvaalensis* (fig. 6F in Hartmann et al. 2011), both with flowers firmly enveloped by the base of the inflorescence forming a solid base on the outside of which the bracts and bracteoles appear as outgrowths.

Also deviating in shape from the majority are *T. crystallina* (fig. 2A in Hartmann et al. 2011) and *T. sheilae* (fig. 1G in Hartmann et al. 2011), both with wide prominent lacinate bracts and bracteoles, visible to the naked eye easily.

Tepals – Tepal tubes lack bladder cells completely in most species, but the surfaces of the free tepal teeth differ distinctly and constantly between species or groups of species.

Most prominent and big are the bladder cells found on tepal teeth of *T. crystallina* (fig. 2A in Hartmann et al. 2011) and *T. sheilae* (fig. 1G in Hartmann et al. 2011), the surfaces resembling those of the leaves in both species.

Also prominent but more elongate bladder cells occur at the tips of the tepals in *T. corallicola* (fig. 8C in Hartmann et al. 2011), resembling also conditions found on the leaves.

The remaining species show in young flowers some bladder cells, in several cases noticeably long, but these can disintegrate with age and also be rubbed off. In old flowers of this type, the tepals can appear smooth.

Further than differences in surfaces, the tepals of different species differ in their relative length and, correlated with this, in the position the tepal teeth take, including also the form of the base of the teeth, i.e. whether they lie smoothly around the tepal tube top or develop bulges at their basal joining points.

All tepal teeth are free by definition, and their tips are formed by pointed protrusions developing from a subapical point, i.e. the tip consists of upper tepal tooth surface tissue only (as is common in members of the subfamily Sesuvioideae). The five tepal teeth of a flower differ in the length of the subapical protrusion, but overall their tips reach more or less the same level above the flower or fruit.

Low protrusions in the shape of bumps or swellings appear prominently in the teapl tips of the tepal teeth of *T. parvifolia* and *T. corymbosa*, visible as raised thick green dots in fresh leaves. In dry herbarium material, it is impossible to recognize the swelling which is mainly caused by highly turgescient cells inside the leaf.

Especially long prominent tepal teeth tips are found in *T. salsoloides* (fig. 6C in Hartmann et al. 2011), and *T. transvaalensis* (fig. 6F in Hartmann et al. 2011), the erect tips reaching 1 mm regularly, hence being visible to the naked eye. Erect tepal teeth of up to 1 mm are also typical of *T. hereroensis* (fig. 10B in Hartmann et al. 2011). In contrast,

the moderately long tepal teeth tips in *T. vleiensis* lean over towards the centre (fig. 9G in Hartmann et al. 2011). In addition, the bases of these longish teeth overlap forming prominent bulges at each incision at the top of the tepal tube. Furthermore, the subapical protrusions are equipped with elongate bladder cells, resulting in a rough aspect.

Tepal teeth less than 1 mm long but also with elongate bladder cells have been found in samples from *T. corallicola* (fig. 8C in Hartmann et al. 2011) and *T. sanguinea* (fig. 7C in Hartmann et al. 2011); in these samples, the bulges at the tepal teeth bases are visible in the scanning electron microscope, yet much less prominent than in the first group.

In a third group of species, the young flowers show erect tepal teeth, but with the ripening of the fruit, the diameter of the operculum increases noticeably. In consequence, the tepal teeth appear relatively shorter and their bases expand the tissue that once formed a bulge in the flower. This ontogenetic change has been observed in *T. corymbosa* and *T. parvifolia*.

A similar development has been traced in the species with big bladder cells on the tepal teeth: *T. crystallina* (fig. 2A in Hartmann et al. 2011), and *T. sheilae* (fig. 1G in Hartmann et al. 2011). At present, the more erect tepal teeth with basal bulges are understood to represent a typical feature of *T. sheilae*, in contrast to the incurving tepal teeth with smooth bases in *T. crystallina*. Observations on the ontogeny are needed to decide whether indeed the described and observed differences are constant or represent developmental states.

Tepal teeth at most 0.5 mm long in most cases form a smooth basal area around the top of the tepal tube, there being no bulges, and this is always correlated with the fact that the teeth lie as a cover overarching the operculum surface in the ripe fruit. It has been said that such teeth can spread in moist conditions, but no experiments have been undertaken to check this. Once the fruit is ripe, however, the teeth can spread widely after the operculum has grown conspicuously in diameter: *T. mozambiquensis*, *T. parvifolia*, *T. sedifolia* (fig. 7G in Hartmann et al. 2011).

In summary, it must be remembered that assessing the tepal teeth needs examination of many, preferably fresh flowers and fruits in detail of several samples, requiring ample material at different ontogenetic states.

Flower colour patterns – As in all members of the subfamilies Sesuvioideae and Aizooideae, the flower has only one series of tepals, lacking petals entirely. Flowers are small in members of *Trianthema* subg. *Papularia*, rarely exceeding 6 mm in diameter, and all elements contribute to forming an optical attraction to possible pollinators. Since not for all species detailed information is available, only some typical combinations of character states can be described at the moment.

In the most widespread species in southern Africa, *T. parvifolia* and *T. vleiensis*, a characteristic model can be demonstrated. The tepals in fresh flowers possess a succulent thick subapical protrusion on the outside, appearing as a green dot when the open flower is looked at. A ring of five dark green dots is in this way presented to the approaching visitor because of the translucent tepal teeth tips. The background colour of the inner tepal surface is white or colour-

less, i.e. a fading green due to the chlorophyll below the epidermis of the inner tepal surface (fig. 4D in Hartmann et al. 2011). The tepal tips can also show some light to darker pink to purple, often more pronounced as a ring around the bases of the tepal teeth or around the tepal tube. The optical ring of attraction is deepened in colour in numerous populations by the formation of purple anthers (fig. 4D in Hartmann et al. 2011), but pink anthers have been found as well. The filaments can be pink, purple, or, in most cases, light yellow, but more conspicuous is the fact that in numerous populations bright orange or purple anthers stand against a paler background colour. Once the anthers open, the pollen is exposed prominently in light yellow, darker yellow, or even in orange. The centre of the flower is marked by a light yellowish-green top of the flower, the later outer rim of the operculum contributing to the pattern of attraction at this state already (fig. 4D in Hartmann et al. 2011).

In the complicated and varying combination of flower colour pattern, no single mode of flower presentation can be determined, but the combination clearly works as an attraction in order to achieve pollination, suggesting strongly that constancy in flower colour pattern is not a means of securing success.

Only in one pair of species have differences in the colour of the inner tepals been used to distinguish species: *T. crystallina* is understood to have small green flowers with diameters about 4 mm whereas *T. sheilae* from the same area possesses bright yellow flowers of 6 mm diameter. It is worth mentioning that *T. sheilae* with usually deep yellow or orange anthers has also been found with scarlet anthers (*Collette* 5026, E).

Overall, it seems that populations follow the same pattern of flower colouring, but it seems at the same time that no strict colour patterns can be related to species as such.

Number of stamens – No more than five stamens have been found in any of the flowers of *T.* subg. *Papularia* examined, but in some species a reduction can be observed: *T. sedifolia* and *T. corallicola* possess only 2–3 stamens. Variable appears the situation in *T. salsoloides*: a single stamen has been found in Kenyan material, two in Tanzanian, but “five or fewer?” in Sudan (*Kotschy* 137, only two found in the isoelectotype material, B).

Operculum – As in most members of the subfamily Sesuvioideae, the fruit of *Trianthema* is a pyxidium, forming an operculum as a lid for the ripe dry capsule, lifting the lid when dry enough, exposing the seeds. In the ontogeny, the surface of the gynoecium in members of *Trianthema* subg. *Papularia* appears flat at first, but early on, the centre seems to be sinking because the rim grows into a broad roll or bulge, like in a certain type of clay bowl.

In *T. sedifolia* and *T. sheilae* from northern Africa, the sunken central part is covered by a layer at the bottom, suggesting a shrinking of the former top layer, resembling in structure linen material creased in a circular arrangement. Rarely, some small splits in this former cover can be seen (*T. sheilae*, fig. 1H in Hartmann et al. 2011).

Four different ontogenetic traits in the development of the fruit including the operculum can be distinguished.

In type 1, a broad rounded outer rim is formed in the opercula of most species, about 400 µm in thickness in young fruits and about 200 µm in old ones, covered by more or less smooth cells and leaving the centre always free. This type of operculum widens conspicuously during the ontogeny, reaching up to 2 mm in diam. and always pushing the rather short tepal teeth outwards while they envelop the rim, the teeth forming a partial cover over the dry ripe fruit (fig. 7G in Hartmann et al. 2011). The centre of the operculum starts off with a small hollow space, resembling the imprint of a thumb with soft slopes. In most cases, these rims are broad and prominent, rough and distinct from the bottom part in *T. crystallina*, *T. sheilae* (fig. 1H in Hartmann et al. 2011). In *T. mozambiquensis* (fig. 11D–E in Hartmann et al. 2011) and *T. sedifolia* (fig. 7G in Hartmann et al. 2011), the rim remains smooth or turns only slightly rough. Independent from the width of the operculum, the base of the pyxidium itself often tapers somewhat towards the base, leaving the fully grown operculum as the widest portion of the whole fruit.

In type 2, the operculum does not widen conspicuously, as is visible in *T. salsoloides*, *T. sanguinea* (fig. 7C in Hartmann et al. 2011), and *T. transvaalensis* (fig. 6D in Hartmann et al. 2011), i.e. the rough rim sits on top of more or less straight sides of the operculum, the tissues of the rim and the sides are uneven and similar to each other. Such opercula are usually equipped with rather long and almost erect pyxidium bases (fig. 7C in Hartmann et al. 2011), equalling the diameter of the operculum or exceeding it only a little.

In type 3, the rim of the operculum remains narrow while the base of the operculum widens conspicuously, the whole top piece resembling a puffed sleeve; similar to type 2, the tissue of the rim differs clearly from the bottom part, visible in *T. corallicola* (fig. 8G in Hartmann et al. 2011) and *T. vleiensis* (fig. 9D in Hartmann et al. 2011). This type of operculum is correlated with a medium long base of the pyxidium (figs 8C & 9G in Hartmann et al. 2011), as opposed to the wide pyxidium in type 1 (fig. 5D in Hartmann et al. 2011).

In type 4, the operculum exposes a smooth basal portion with straight or concave sides overtopped apically by a rim formed by a broad band of much rougher cells as if crocheted with thicker material and a bigger needle. This top can remain sleeve-like or become flat resembling a ruff as worn by Hanseatic ministers and senators in shape, but not pleated. The opercula of *T. parvifolia* (fig. 4F), *T. corymbosa* (fig. 4C), and *T. hereroensis* (fig. 10D, all figures in Hartmann et al. 2011) show this type; the difference in the rough upper rims is similar to that found in type 3.

Most opercula of the African species exceed rarely 1 mm (*T. mozambiquensis* can reach 1.5 mm) in diameter, difference in size can, therefore, not be used as a distinguishing feature.

Seeds – Two seeds are usually found in a pyxidium of *Trianthema* subg. *Papularia*, placed on top of each other (fig. 6F in Hartmann et al. 2011), one sometimes held in the lower portion and the other dispersed with its operculum. In many species, however, the two seeds are dispersed as a double package (e.g. *T. sedifolia*, fig. 7H in Hartmann et al. 2011), sticking together at their flat contact zones for some time.

This contact area can be flat or even smooth, but the opposite outer side can bear some ornamentation in the shape of ridges or crests. As long as the aril covers the seed, the crests are smooth-edged and soft (figs 7D, 7H & 8D in Hartmann et al. 2011), later they appear more sharp-edged and more distinct, especially in the upper region in side view (figs 3E & 11F in Hartmann et al. 2011). The ridges on the side of the seed lie vaguely semi-circular, but they can also stop short or deviate from the regularly bending shape. Differences and variation are much less than in the species of *Trianthema* subg. *Trianthema* (Hassan et al. 2005a, Prescott 1984).

A single seed per pyxidium is reported for *T. salsoloides* from NE Africa, a species very similar to *T. tranvaalensis* from NE South Africa, in which latter often an abortive second seed is found. A single seed was also found in pyxidia of *T. corymbosa* as a rare deviation.

Smooth seeds have been found in samples of *T. sedifolia* (fig. 7H in Hartmann et al. 2011), *T. hereroensis*, and *T. corallicola* (fig. 8D & H in Hartmann et al. 2011), but some seeds with low ridges have also been met with in these species.

Ripe seeds are usually dark brown to black, the shape in side view is oval to almost circular. The maximum length of seeds lies between 0.8 and 1.4 mm, permitting some groupings of species: smallest seeds of 0.8–0.9 mm have been found in *T. parvifolia* and *T. corymbosa*. Medium sized seeds of 1–1.2 mm length predominate in *T. corallicola*, *T. mozambiquensis*, *T. sanguinea*, *T. sedifolia*, *T. sheilae*, and *T. vleien-sis*. Big seeds of 1.3 mm minimum length, reaching up to 1.5 mm, have been found in *T. transvaalensis* in Africa only. There are overlaps between the size classes, and seeds alone cannot be used to identify a species.

DISCUSSION

Considerations on phytogeography and species groupings in Africa

While *T.* subg. *Trianthema* has a distinct centre of diversity in Australia (Prescott 1984), Africa and the adjacent parts of Arabia represent the areas with most species (twelve) in *T.* subg. *Papularia*. The chorology of the African species is here interpreted in terms of the system of White (1983, 1993) and its later emendations (Jürgens 1991, White & Léonard 1991, Clarke 1998).

Six species are found in NE Africa and the southwestern part of Arabia (fig. 13 in Hartmann et al. 2011). The most northern species, *T. sheilae*, is endemic to the Saharo-Sindian Regional Zone and is reported for the Sahara as well. No proof has been found for this, and the occurrence to the west of the known area must be considered as being inadequately documented. Five other species are elements of the Somali Masai Regional Centre of Endemism, *T. sedifolia* being the most widespread one also transgressing into the Sahel Regional Transition Zone and the Swahilian Regional Centre of Endemism; one cannot decide at this date whether the large gap in the distribution of this species – an outpost in the western part of the Sahel – is a chorological reality

or the result of undercollecting. The four other species have much more restricted distributions: *T. crystallina* is restricted to the Arabian extension, *T. corallicola* to the African coastal areas in the south of the phytochorion, while two species (*T. salsoloides* and *T. sanguinea*) only occur in the south of the Somali Masai Regional Centre of Endemism.

Members of the subgenus are completely absent from the Zambezian Regional Centre of Endemism, apart from one outpost of *T. salsoloides* in the very north of this phytochorion.

The other six species are restricted to the southern part of Africa:

- *T. mozambiquensis*, being restricted to the Swahilian/Maputaland Regional Transition Zone, seems to occur only in the southern coastal area, while *T. vleien-sis*, however, forms part of the western part of the Kalahari Highveld Regional Transition Zone, strictly separated from *T. transvaalensis* with a distribution area further north east and transgressing into neighbouring phytochoria.
- The three remaining species are elements of the Nama Karoo Region, *T. parvifolia* being widely distributed there and somewhat penetrating into neighbouring phytochoria. In contrast, *T. corymbosa* (Eastern Gariep District) and *T. hereroensis* (Namib District) grow in much restricted areas, being endemic there.

Although it is obvious that not a single species has been found in the north and in the south, no character expressions have been found that would support the separation of the geographically separated groups of species (electronic appendix 1). In contrast, a number of features appears in southern and northern species, e.g. the smooth wide operculum in *T. sedifolia* in the north and *T. mozambiquensis* in the south, demonstrating similarities over a wide distance. Groupings based on morphological similarities are discussed below.

A group restricted to the north stands out in having big globose bladder cells of about 160 µm in dense or looser arrangement on the internodes and of about 200 µm diam. in a dense layer on leaves and tepal teeth, forming a secondary surface on the two latter organs, both apically rounded. *T. crystallina* (fig. 2A–C in Hartmann et al. 2011.) and *T. sheilae* (fig. 1E–H in Hartmann et al. 2011) belong in this group, the first differing from the second only in width of flowers and the colour inside the tepals. In order to assess whether indeed two taxa at species rank are involved, more and especially living material will be needed. It must be mentioned, however, that the same leaf and internode surfaces occur also in *T. argentina* (fig. 1A–C in Hartmann et al. 2011), the only species of the subgenus in the Americas.

A third species in northern Africa, *T. sedifolia*, shares with the three mentioned species the big bladder cells on the internodes and has a wrinkled layer of tissue at the bottom of the central deepening of the operculum, a feature also found in *T. crystallina* (fig. 2A–C in Hartmann et al. 2011.) and *T. sheilae*, but combined with a smoother rim of the operculum in most cases.

Most similar to *T. sedifolia* is *T. mozambiquensis*, known only from one population in Mozambique (fig. 13 in Hartmann et al. 2011), especially in the possession of short te-

pal teeth overarching the ripe operculum but not covering it completely.

The smooth operculum ring and wrinkled bottom layers in the centre of the operculum are also found in all species growing further east, from Pakistan over India around the Gulf of Bengal and in Australia (Hartmann et al. 2011), where the layer develops into a sail-like cover over the interior of the operculum. All this material has in the past been named *T. triquetra*, including the relevant African material.

Another group can be distinguished in southern Africa, comprising *T. corymbosa* (fig. 4C), *T. hereroensis* (fig. 14D), and *T. parvifolia* (fig. 4F, all figures in Hartmann et al. 2011). All populations included here are characterized by the development of very rough rims of the operculum consisting of big elevated cells, resembling a short crocheted sleeve made up of thicker material knitted with a thicker needle above the almost smooth base of the operculum. In some cases, the rim lies flat towards the sides, possibly a feature developing later during the ripening.

Of the three species, *T. corymbosa* (fig. 4C in Hartmann et al. 2011) is the only deciduous taxon known until now in *T.* subg. *Papularia*. *T. parvifolia*, on the other hand, is unique in keeping the prominent broad flaps along the petioles longer than the blades on the persisting stems (fig. 4E in Hartmann et al. 2011). In this species, however, the northern populations are of uncertain taxonomic rank. The occurrence of bladder cells in such samples might indicate that another taxon at species rank may possibly be found, but the amount of available material and data from northern Namibia and southern Angola are too sparse to permit a decision at this state. *T. hereroensis* (fig. 14D in Hartmann et al. 2011), however, can be clearly distinguished by its acuminate leaf tips. Some opercula of *T. sanguinea* agree with this type from southern Africa, but again more material is needed to decide finally.

A third group comprises plants with a distinct clear longitudinal green line along the entire upper leaf surface, white in translucent light and dark green in incident light. In contrast to groups 1 and 2, the leaf tips are acuminate and hence pointed, and the tepal teeth possess prominent bulges at the base of the incisions between them. *T. transvaalensis* and the new species *T. vleiensis* (fig. 9E in Hartmann et al. 2011) can be placed in this group, sharing also the possession of tepal tips up to 1 mm in length adorned with elongate papillae. *T. vleiensis* forms most striking opercula shaped like short puffed sleeves with a rather narrow rim on top of a basally widening base of the operculum, clearly a synapomorphy of the species (fig. 9G in Hartmann et al. 2011). The species has shiny smooth leaf surfaces and only few bladder cells on the internodes and rather wide flaps along the petioles. *T. transvaalensis* differs distinctly in forming compact solid bases of the inflorescences into which the bases of the flowers appear to be sunken (fig. 6F in Hartmann et al. 2011), with tiny bracts and bracteoles on the solid tissue of the compact bases. The operculum has straight sides ending in a somewhat broader rim on top, the cells inconspicuously rough and not as distinct as in *T. vleiensis*; of the two seeds per pyxidium, one is often abortive and reduced in size in

T. transvaalensis, which also is remarkable in showing elongate papillae on leaves and internodes.

T. salsoloides may also belong in this group, showing all features described above for *T. transvaalensis* except for the fact that a single seed is found in the former species. A final decision cannot be taken yet because no fresh material allowing an assessment of the upper leaf surface of *T. salsoloides* is available.

The new species *T. corallicola* cannot be placed in any of the groups, deviating from all other known species in having a more or less dense cover of bladder cells growing into 500 µm long hairs on the internodes, covering it like fur, the longest ever found in *T.* subg. *Papularia*. The leaves and the tepal teeth are also hairy, especially the tips, but these bladder cells reach only 200 µm in length (fig. 8 in Hartmann et al. 2011). The opercula shaped like puffed sleeves resemble those of *T. vleiensis* most closely, which, however, lack prominent bladder cells completely on the leaves and show only a very sparse occurrence of small globose bladder cells on the internodes.

In summary, the presently accepted species can be distinguished and described reliably, but groups are not necessarily clear-cut since too many similarities exist that could be interpreted as apomorphies as well as parallel evolutionary lines.

Considerations on ecological parameters

A species with a very restricted area of distribution is represented by *T. hereroensis*, found near the coast in the Namib, separated from populations placed in *T. parvifolia* but widely surrounded by that latter species. Material known until now is reported to grow in river sand, suggesting that soil conditions may restrict the suitable region in which the species can settle.

Only for few populations, measurements are available of the pH in the soil, but they confirm observations in habitats: *T. vleiensis* grows in alkaline soil with a pH of 8–9 while for *T. parvifolia* pH values of 5–7 have been measured. Both species share the growth form of a perennial decumbent plant, living for many years forming stems of up to 12 mm in diameter, differing in this character set from the more western and the more eastern species.

Worth considering is also the fact that only *T. hereroensis* and *T. corymbosa* expect rain in winter solely; the morphologically similar species *T. parvifolia* grow just east of the winter rainfall boundary, receiving rainfall in March and November over most of its area, although February and March rains can also be tolerated.

In summary, it can be concluded that the southern and the northern species of *T.* subg. *Papularia* are so distinctly separated by a wide gap over the tropics that a common ancestor must be imagined to have existed a long time ago. In contrast, the winter rainfall species in the south have probably evolved relatively late together with the establishment of the winter rainfall as such, and *T. vleiensis* seems to settle in restricted areas with most alkaline soils. Surely, such speciation is locally adapted to prevailing conditions on the spot.

Artificial key to the species of *Trianthema* subg. *Papularia*

1. Leaf blades and tepal teeth covered completely by big globose bladder cells, bracts and bracteoles fimbriate.....2
- 1'. Leaf blades and tepal teeth smooth from inconspicuous bladder cells or acuminate bladder cells as short hairs in loose arrangement.....3
2. Tepals yellow inside, flowers 6 mm wide; reported from NE Africa, SW Arabia and Yemen.....10 *T. sheilae*
- 2'. Tepals green inside, about 4 mm wide; recorded only from SW Arabia and Yemen.....3 *T. crystallina*
3. Plants deciduous in the dry season, pedicels elongating during fruit ripening; only near the mouth of the Gariep River in South Africa and Namibia.....2 *T. corymbosa*
- 3'. Plants with leaves during the dry season.....4
4. Flowers basally embedded in the bottom of the inflorescence, the inflorescence breaking off as a whole; bases of tepal teeth forming prominent bulges on the otherwise straight erect long sides of the flower.....5
- 4'. Flowers basally free, breaking off individually; without or with inconspicuous bulges at the bases of the tepal teeth.....6
5. Two seeds per pyxidium, sometimes the basal one not fully developed; from S Zimbabwe through the old Transvaal Province and into KwaZulu/Natal, South Africa.....11 *T. transvaalensis*
- 5'. Only one seed inside the pyxidium; in a N-S band through the west of Kenya and Tanzania.....7 *T. salsoloides*
6. Internodes and leaf blades with elongate acuminate bladder cells like hairs visible to the naked eye; only along the southern coast of Somalia and the northern coast of Kenya.....1 *T. corallicola*
- 6'. Internodes with low and inconspicuous bladder cells, never eye-catching.....7
7. Pseudo-stipules to both sides of the petiole rounded, the pair forming a broad ellipse; tepal teeth as long as the basal tepal tube, erect; only known from sandy riverbeds in Namibia near the coast.....4 *T. hereroensis*
- 7'. Pseudo-stipules more or less angular, broad and spreading, usually ending in a short broad tooth.....8
8. Tepal teeth straight with distinct small finger-shape bladder cell.....9
- 8'. Tepal teeth curving over the pyxidium top to various degrees.....10
9. Operculum with a smooth broad rounded rim; only in SE Kenya and adjacent parts of Tanzania.....8 *T. sanguinea*
- 9'. Operculum shaped like a puffed-sleeve; only in the central plateau of South Africa.....12 *T. vleiensis*
10. Base of leaf persisting as a white sheath with several layers of pseudo-stipules along the stem; from Namibia to the Great Karoo in South Africa.....6 *T. parvifolia*
- 10'. The pseudo-stipules at the base of the leaves short-lived and brittle, decaying soon.....11
11. Pseudo-stipules ending in a rectangle pointing outwards; only known from coastal southern Mozambique.....5 *T. mozambiquensis*
- 11'. Pseudo-stipules with an oblique edge adorned with a short tooth more or less in its middle; from Morocco to SW Arabia and Yemen.....9 *T. sedifolia*

TAXONOMIC TREATMENT

Trianthema L. subg. *Papularia* (Forssk.) Jeffrey (Jeffrey 1960: 237). – Type: *T. crystallina* (Forssk.) Vahl

Annual to perennial plants, perennial plants also flowering as annuals in several species, rarely deciduous, branches erect, decumbent, procumbent, but never with adventitious roots, internodes densely to sparsely papillate from bladder cells, smooth and woody with age, white over yellow to brown and black. Leaves with more or less prominent and elaborate pseudo-stipules along the petiole, blades always wider than thick, epidermis with prominent to inconspicuous bladder cells. Inflorescences rather dense appearing axillary and almost compact, with five and more flowers, only

in young plants also at first single-flowered. Flowers with subapical thickenings or subapically placed enations overtopping the actual tepal tip in shape of acuminate protrusions on the free tepal teeth, the tepal bases forming a tube connate with the base of the unilocular ovary, containing 2 ovules, rarely only one. Stamens 1–5 in alternitepalous positions, never more stamens, anthers and pollen often in contrasting bright colours; gynoecium with a single stigma in the centre which is surrounded by a broad solid rim around its outer edge. Fruit developing into a pyxidium, the operculum always with a prominent persisting rim, the base either with vertical sides or oblique after the rim has been pulled together like a puffed sleeve. Seeds mostly two on top of each other, rarely only one.

1. *Trianthema corallicola* H.E.K.Hartmann & Liede (Hartmann et al. 2011: 195). – Type: Somalia. Shabellaha Hoose, 2–3 km S of Marka [Merka] along the road to Shalaanbood [Shalambod], 14 Jun. 1987, Friis, Vollesen & Hassan 5029 (holo-: C; iso-: B, K). Fig. 8 in Hartmann et al. 2011: 196.

Habitat and distribution – In sandy patches on coral reefs along the coast of S Somalia and N Kenya; found also further inland on gypsum in S Somalia.

Chorology – Endemic to the coastal area of the Somali-Masai Regional Centre of Endemism (White 1983).

Note – The species presents a sample for a small distribution area obviously restricted by soil conditions, here along the coast of Somalia and Kenya, but morphologically distinct and unique in the subgenus.

2. *Trianthema corymbosa* (Sond.) H.E.K.Hartmann & Liede (Hartmann et al. 2011: 197) – *T. crystallina* (Forssk.) Vahl var. *corymbosa* E.Mey. ex Sond. in Harvey & Sonder Flora Capensis: 598. 1862 (Sonder 1862); *T. parvifolia* Sond. var. *corymbosa* Adamson (Adamson 1962: 251). – Type: South Africa, Northern Cape, Gariep, Verleptpram, under 1000 Fuss, Sep., Drège s.n. 04-457 (lecto-: S; designated by Adamson 1962: 251). Fig. 4A–C in Hartmann et al. 2011: 185.

Trianthema crystallina (Forssk.) Vahl var. *rubens* E.Mey. ex Sond. (Sonder 1862: 598). – *T. parvifolia* Sond. var. *rubens* Adamson (Adamson 1962: 251). – Type: South Africa, Northern Cape, Gariep, Verleptpram, under 500 Fuss, Sep., Drège s.n. S 04-455 (lecto-: S; designated by Adamson 1962: 251).

Habitat and distribution – In open, sandy, stony, gravelly soils mainly below quartz or granite slopes and in disturbed places in the lower ranges near the mouth of the Gariep River, Northern Cape Province, South Africa. Alt. 240–930 m.

Chorology – Endemic to the Eastern Gariep District of the Nama Karoo Region (Jürgens 1991) with a centre at the mouth of the Gariep River.

Notes – Features distinguishing *T. corymbosa* from *T. parvifolia*, under which latter name the former taxon was kept as a variety by Adamson (1962), are the deciduous leaves, the loose arrangement of the flowers in the ripe fruit state, and the erect tepal teeth when the fruit is ripe. All these character states support the distinction of the taxon at species level, and the name *T. corymbosa* has been chosen.

3. *Trianthema crystallina* (Forssk.) Vahl (Vahl 1790: 32). – *Papularia crystallina* Forssk. (Forsskål 1775: 69). – Type: Saudi Arabia, Forsskål C III.14 (holo-: C). Fig. 2A–C in Hartmann et al. 2011: 182.

T. crystallina (Forssk.) Vahl var. *suberosa* Terracciano (Terracciano 1894: 108). – Type: Eritrea, I Midir, 22 Mar. 1892, Terracciano 187 (lecto-: FT; seen in Aluka).

T. crystallina (Forssk.) Vahl var. *obscura* Armari (Armari 1904: 146). – Type: Eritrea, Baia de Anfilah, 23 Mar. 1892, Terracciano 51 bis (lecto-: FT; designated by Hartmann 2001: 332; seen in Aluka).

Habitat and distribution – In open, sandy, stony, gravelly, and disturbed places, mostly at or near the sea along the West

Coast of Yemen and SW coastal areas of Saudi Arabia. Alt. 0–560 m.

Chorology – Probably endemic to the S Arabian extension of the Somali-Masai Regional Centre of Endemism (White & Léonard 1991).

Notes – Attention must be drawn to the fact that northern African material of *T. sedifolia* has often been named *T. crystallina* in error. The former species has, however, a tendency to expose the operculum in ripe state while the tepal teeth spread at the same time; yet, it can easily be distinguished from *T. crystallina* by its slender darker leaves with only moderately elevated semi-orbicular bladder cells not overlapping each other when dry. On the other hand, *T. sedifolia* shares with *T. crystallina* the prominent and numerous bladder cells on the internodes.

The present investigations permit the conclusion that *T. crystallina* in the sense of the type of Forsskål (C) has a restricted distribution on the SW Arabian peninsula and has not been documented reliably from other areas. The species is most similar to *T. sheilae*, both taxa sharing several character states.

T. crystallina forma *suberosa* Terracciano (1894) and *T. crystallina* f. *obscura* Armari (1904) from Eritrea are included here, based on evidence from images available in Aluka; the original material at FT was not made available for examination. Evidence, however, is insufficient from the electronic images, hence the occurrence of *T. crystallina* in Eritrea remains uncertain.

4. *Trianthema hereroensis* Schinz (Schinz 1897: 76). – Type: Namibia, !Kuseb, 1886, Stapf s.n. (lecto-: Z). Fig. 10A–D in Hartmann et al. 2011: 200.

Habitat and distribution – In river sand in the coastal plains of Namibia. Alt. 30 m.

Chorology – Endemic to the Namib District of the Nama Karoo Region (Jürgens 1991).

Notes – No further collections can at this date be identified as *T. hereroensis*, and the distribution must at the moment be understood to be restricted to the lower sandy river beds of the Namib desert.

The species differs clearly from *T. parvifolia*, with which it has been united by Adamson (1962), in having pointed acuminate leaf tips and pseudo-stipules along both sides of the petiole forming almost an oval shape, apically truncate and almost touching the base of the blade there; in having erect long tepal teeth formed mainly by the very long subapical protrusions of the tepals, never arching over the flower or the fruit; and finally, in having very smooth and shiny black seeds.

Curtis (1985) listed *T. hereroensis* as one of the major hosts of honeydew producing scale insects (Homoptera: Coccoidea), the main food source for the desert ant *Camponotus detritus* Emery.

5. *Trianthema mozambiquensis* H.E.K.Hartmann & Liede (Hartmann et al. 2011: 202) – Type: Mozambique, Lourenço Marques, Matola, km 28,3 de Boane para Porto Henrique,

picada a esquerda (links) para a propriedade de Augusto Fonseca ao km. 6,2 (Cq), 28 May 1971, *Marques* 2299 (holo-: WAG). Fig. 11 in Hartmann et al. 2011: 201.

Habitat and distribution – unknown, Mozambique, Lourenço Marques. Only known from the type collection

Chorology – Endemic to the Swahilian/Maputaland Regional Transition Zone (Clarke 1998), but not in Pondoland.

Notes – Differs from all other species in southern Africa in having opercula with broad smooth rims like ring-walls perpendicular on the outside, not widening there; most similar to *T. sedifolia* from northern Africa in having distinctly papillate internodes and in operculum shape, but differing from the latter in possessing broader, strictly rectangular pseudo-stipules with a prominent tooth.

6. *Trianthema parvifolia* E.Mey. ex Sond. (Sonder 1862: 598). – *T. triquetra* Willd. ex Spreng. subsp. *parvifolia* (E.Mey. ex Sond.) Jeffrey (Jeffrey 1960: 237). – *T. parvifolia* E.Mey. ex Sond. var. *parvifolia* (Adamson 1962: 250). – Type: South Africa, Western Cape, Gamka River, Zwartbulletjie, 1837, *Drège* s.n. as S 03-525 (lecto-: S, designated by Adamson 1962: 250). Fig. 4D–F in Hartmann et al. 2011: 185.

Trianthema parvifolia E.Mey. ex Sond. var. *annulata* Adamson (Adamson 1962: 251). – Type: Namibia, Achterfontein, on sanddunes, 11 Dec. 1915, *Pearson* 9231 (holo-: K).

Habitat and distribution – In open, sandy, stony, gravelly, and disturbed places in Angola, Botswana, Namibia, western parts of the Northern Cape Province and Western Cape Province, South Africa. Alt. 500–1600 m.

Chorology – Near-endemic to the Nama Karoo Region (Jürgens 1991), transgressing into neighbouring phytochoria.

Notes – Examination of the type material of *T. parvifolia* var. *annulata*, *Pearson* 9231, reveals that the material was collected at a particular state during the seasonal circle: the leaf blades are broken off while the basal portions of petiole and the very broad pseudo-stipules clasping the stem remain visible, described as “white rings”. Depending on weather conditions, this phase can last for some time in habitat and can hence be observed in many populations of *T. parvifolia*.

Some populations in the northern part of the distribution area differ from typical *T. parvifolia* in having longer, more papillate leaf blades, internodes with globose bladder cells, a rather thin undulating rim of the operculum and, in some cases, longish seeds in contrast to the roundish seeds found in both named species. It appears, however, that the changes occur in steps and gradually, perhaps representing a cline. With only little and old herbarium material available, no conclusions can be drawn at this stage, but the northern and north-eastern populations need further attention and more extensive study based on fresh material.

7. *Trianthema salsoloides* Fenzl ex Oliver (Oliver 1871: 588). – Type: Sudan, “Ad pagum Cordofanum Arasch Cool inter gramina locis siccis. U.i.1841. glareosis d.”, 7 Oct. 1839, *Kotschy* 137 (lecto-: K, electronic image K000075434;

iso-: B, BM, BR, M, WAG). Fig. 6 D–F in Hartmann et al. 2011: 187.

Trianthema multiflora Peter (Peter 1932: 29). – Type: Tanzania, Masai District, Emugur Belekj, alt. 870 m, 15 Jul. 1926, *Peter* 42741a (lecto-: B).

Habitat and distribution – In ruderal, open places with grass to scrub cover, mostly in alluvial loamy or black cotton soil on which sometimes pebbles can be found from Kordofan in Sudan (only the type of *Kotschy* known from there) through Kenya into Tanzania. Alt. 320–1700 m.

Chorology – Endemic to the southern part of the Somali Masai Regional Centre of Endemism (White 1983).

Notes – Fenzl distributed material of *Kotschy* 137 with the inscription “*Trianthema salsoloides* Fenzl”, but never published a description. Oliver (1871: 588) gave “Fenzl in Herb. *Kotschy*. Nub. 137” behind the name “*T. salsoloides*”, yet he did not annotate the relevant sheet at K as a type. Nevertheless, Oliver must have seen the sheet kept now at K, where he worked, and this particular sheet is chosen here as the lectotype. All other sheets of *Kotschy* 137 in other herbaria are isotypes.

8. *Trianthema sanguinea* Volken & Irmsch. (Volken & Irmscher 1913: 498). – *T. triquetra* Willd. ex Spreng. subsp. *triquetra* var. *sanguinea* (Volken & Irmsch.) Jeffrey (Jeffrey 1960: 237). – Type: Tanzania, Moshi District, Steppe zwischen Pangani- und Himofluß, alt. 700 m, 5 Jul. 1893, *Volken* 458 (holo-: B; iso-: BR, K). Fig. 7A–D in Hartmann et al. 2011: 189.

Trianthema nigricans Peter (Peter 1932: 30). – Type: Tanzania, Masai District, Emugur Belekj, alt. 870 m, 15 Jul. 1926, *Peter* 42741c (holo-: B).

Habitat and distribution – In open, disturbed places among pebbles in SE Kenya and NE Tanzania. Alt. 15–350 m.

Chorology – Endemic to the southern part of the Somali Masai Regional Centre of Endemism (White 1983).

Notes – Remarkable is the rather small distribution area along the border between Kenya and Tanzania and rather close to the coast.

9. *Trianthema sedifolia* Vis. (Visiani 1836: 19, t. 3, fl.). – *T. crystallina* (Forssk.) Vahl var. *sedifolia* (Vis.) Hiern (Hiern 1898: 415). Type: Sudan, Khartoum, *Brocchi* s.n. (holo-: BASSA, n.v.). Fig. 7E–H in Hartmann et al. 2011: 189.

Trianthema sedifolia Vis. var. *microphylla* Courbon (Courbon 1862: 156). – Type: Eritrea, Dahlak Island, Dessie (Dissée), lieux argilleux de la plaine du village, *Courbon* s.n. (holo-: P, n.v.).

Trianthema glandulosa Peter (Peter 1932: 30). – Type: Tanzania, Masai District, Emugur Belekj, alt. 870 m, 15 Jul. 1926, *Peter* 42741b (holo-: B).

Habitat and distribution – In open, disturbed places among pebbles in Saudi Arabia, Yemen, Morocco, Mauritania, Eritrea, Somalia, Sudan, Kenya, northern Tanzania, Uganda. Alt. 5–1000 m.

Chorology – Pluriregional species occurring in the Sahel Regional Transition Zone, the Somali Masai Regional Centre of Endemism including its Arabian extension, and the Swahilian Regional Centre of Endemism (White 1983, White & Léonard 1991).

Notes – *T. sedifolia* shares with *T. crystallina* and *T. sheilae* the big prominent and numerous bladder cells on the internodes but lacks the big globose bladder cells on the leaves of the two latter species completely. *T. sedifolia* differs also in its annual growth, the possession of more narrow and acute bracts and bracteoles, and in the formation of almost smooth seed surfaces from the two other species in the area.

The obvious gap in distribution between the southern and the northern parts of the NE African area can, on one hand, be explained by the existence of the Ethiopian Highlands, probably unsuitable for the genus to grow, and also by the fact that no collections from southern Sudan are available, neither recent nor older. A record from Morocco (Müller s.n., B) cannot be located precisely, but it suggests that the species is much more widespread in northern Africa than hitherto reported reliably. Nevertheless, the presently known data show a wide distribution area for this species.

10. *Trianthema sheilae* A.G.Mill. & J.A.Nyberg (Miller & Nyberg 1994: 33). – Type: Saudi Arabia, 12 km N of Mukayl road junction Jizan-Qunfudhah road, 4 Feb. 1984, *Collenette* 4718 (holo-: E). Fig. 1E–H in Hartmann et al. 2011: 180.

Habitat and distribution – Most often in sand near the sea, amongst lava rocks or coral remains, more rarely inland and in loam near the western coast of Saudi Arabia and along the southern coast of Yemen, in southern Egypt, eastern Sudan, and southern Eritrea. Alt. 10–2100 m.

Chorology – Endemic to the Saharo-Sindian Regional Zone (White & Léonard 1991), with some outposts in neighbouring phytochoria to the south.

Notes – *T. sheilae* was described as differing from *T. crystallina* in being a much-branched, ascending bushy annual or perennial herb, having yellowish-green leaves and yellow flowers. Since Forsskål (1775) described the habit of *T. crystallina* as “fruticosa”, he obviously saw a shrubby plant from which he picked a branch, which looks woody and whitish on the type, suggesting perennial growth. Fresh material from Sudan combines decumbent branches with yellow flowers, as reported also for Eritrean material. Furthermore, all plants with appropriate records mention yellowish-green leaves, independent from habit. In the discussion of *T. sheilae*, it is reported that the tepal teeth spread in *T. crystallina*, a character state not visible on the type sheet of the latter species. Here, the tepal teeth stand erect and only a little connivent in flowers pressed sideways, but they cover the operculum completely in those flowers that were pressed from the top.

T. sheilae is very similar to *T. crystallina*, as is obvious from the list of shared character states under *T. crystallina*. Differences lie in the bigger fresh flowers with yellow inner tepal surfaces (6 mm diam. in *T. sheilae* as opposed to 3 mm in the fresh flower of *T. crystallina*), the fact that the outer tepal lobes exceed the tepal tips distinctly, the formation of “sinuses” at the bases of the tepal lobes, actually represent-

ing thickened loops in the closed flower - not visible in the open flower, and the possession of a long stigma reaching up well between the stamens (all described character states for *T. sheilae*).

The most prominent features, the bigger and yellow flowers in *T. sheilae*, lose their size and special colour when being dried, and hence an assessment of herbarium material is extremely difficult, leading to misidentifications. Since the differences are indeed small, it may be worth considering whether the two taxa should not better be ranked as two subspecies in one species, *T. crystallina*.

11. *Trianthema transvaalensis* Schinz (Schinz 1915: 396). – Type: *T. salsoloides* var. *transvaalensis* (Schinz) Adamson (Adamson 1962: 248). Type: South Africa, Transvaal, in arenos prope Matsaba, alt. 730 m, 4 Mar. 1897, *Schlechter* 4876 (holo-: Z; iso-: K). Fig. 6D–F in Hartmann et al. 2011: 186.

Trianthema salsoloides Fenzl ex Oliver var. *stenophylla* Adamson (Adamson 1962: 249). – Type: South Africa, Transvaal, Kruger National Park, Gudjane Rd on turn, 20 Apr. 1954, *van der Schijff & Marais* 3734 (holo-: K; iso-: PRE).

Habitat and distribution – In open places with grass to scrub cover, mostly in alluvial loamy or black cotton soil from Botswana, the southern parts of Zimbabwe and through Limpopo Province, Mpumalanga, and KwaZulu/Natal, South Africa into Mozambique. Alt. 100–200 m.

Chorology – Near-endemic to the Kalahari-Highveld Regional Transition Zone (White 1983), passing also into neighbouring phytochoria.

Notes – Adamson (1962: 248–249) placed *T. transvaalensis* as a variety in *T. salsoloides*, describing the former as being 50 cm tall, a feature that cannot be confirmed with fresh material; but branches may be 50 cm long, yet these are decumbent to prostrate. Both species share three character states: (1) the possession of prominent bulges at the bases of the tepal teeth, (2) the formation of long bladder cells at the tips of the long, erect subapical horns, and (3) the deeply placed bases of the ovaries at least partially connate.

Conspicuous features present in *T. transvaalensis* and absent in *T. salsoloides* are: (1) the existence of a prominent translucent line along the upper leaf surface combined with a shorter one along the lower leaf surface, (2) the only basally connate flowers and fruits in the lateral densely glomerulate inflorescences, (3) the more densely papillate leaves and internodes, and (4) the operculum resembling a short puffed sleeve when ripe.

The type of *T. salsoloides* var. *stenophylla* shows all features critical for *T. transvaalensis*. It must be noted in this respect that older internodes of *T. transvaalensis* turn smooth with age and that the tepal tips or horns exceed the length of the tepal teeth only in very newly opened flowers, hence no differences remain to justify the upholding of a separate species.

Little material is available for investigation, and it is remarkable that the three collections from lowlands in KwaZulu/Natal agree with the critical features, albeit they occur in a hotter and more tropical climate than those from the

highlands of Zimbabwe and the Limpopo Province of South Africa.

12. *Trianthema vleiensis* H.E.K.Hartmann & Liede (Hartmann et al. 2011: 211). – Type: South Africa, North West Province, Bloemhof, S.A.Lombard Nature Reserve, alt. 1240 m, 9 Mar. 1993, *Hartmann* 31323 (holo-: HBG). Fig. 9 in Hartmann et al. 2011: 198.

Habitat and distribution – Always at the upper edges of salt pans (“vleis” in Afrikaans) in grassland or open scrub, very often with some limestones on top of the fine soil in SE North West Province, NW Free State, and NE Northern Cape Province, South Africa. Alt. 1200–1400 m.

Chorology – Endemic to the western part of the Kalahari Highveld Regional Transition Zone (White 1983), well separated from *T. transvaalensis*.

Notes – At first sight, the plants resemble *T. transvaalensis* in having elongate acuminate leaves with a distinct dark longitudinal line along the upper leaf surface, a feature distinguishing the group of populations clearly from *T. parvifolia* with only dotted leaves with rounded tips. Unique to this species are the rather narrow pseudo-stipules and the moderate bulges at the bases of the tepal teeth – *T. parvifolia* lacks any protrusions at the bases of the tepal teeth, and *T. transvaalensis* has prominent ones, resembling *T. salsoloides* from northern Africa. The populations of *T. vleiensis* settle in an area between the regions in which *T. transvaalensis* and *T. parvifolia* grow, clearly separated and typically at the upper edges of vleis, i.e. salt pans with varying water table, i.e. they inhabit extrazonal habitats. The epithet is chosen after this typical habitat.

SUPPLEMENTARY MATERIAL

Supplementary data are available in Excel format at the Supplementary Data Site of publications from the National Botanic Garden of Belgium (<http://www.nbgpublisher.be> > SBB50 > folder 667) and consist of a list of characters and their expressions in the African species of *Trianthema* subg. *Papularia*.

ACKNOWLEDGEMENTS

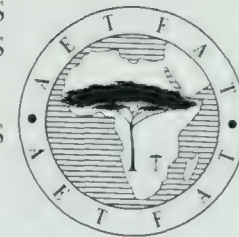
HEKH acknowledges gratefully funding of field work in Africa from 1969 until 2007 by Deutsche Forschungsgemeinschaft 1969–2003, by the National Botanic Gardens of South Africa in several years, by the donation of the Kirstenbosch Jubilee Fellowship in 1977, by the Hamburgische Wissenschaftliche Gesellschaft in 1980 and 1981, by the University of Hamburg in several years, and by Prof. Dr. W. Hartmann, Hamburg. Permission to collect and export material for study in Hamburg was granted by the Nature Conservation bodies of Botswana, Kenya, Namibia, Tanzania, the Provinces of South Africa, and of Sudan and Zimbabwe. Many students and farmers have helped to find populations, and colleagues from the universities of Khartoum (Sudan, Prof. Ekhlal Abdel Bari), Nairobi (Kenya University, Prof. L.E. Newton), Pretoria (including also SANBI), Stellenbosch (Prof. Sue Milton) have supported the field work extensively over many

years. To all, HEKH extends her cordial thanks for making possible such a long-lasting and far-reaching project, started in 1977. Thanks go also to Marco Fischer for developing the programme Taxo 2Map. Prof. Dr. E. Robbrecht is thanked for additions with respect to the phytochoria the African species occur in. The directors of the herbaria of AD, B, BRI, C, DNA, E, HBG, K, L, MO, UTB, WAG, and Z are thanked for loans of valuable sheets, including type material, and most of them for permission to study some samples under the SEM.

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- Manuscript received 13 Jul. 2011; accepted in revised version 5 Nov. 2012.
- Communicating Editor: Elmar Robbrecht.
- A longer version of this manuscript was published in *Plant Ecology and Evolution* 144(2), pages 177–213.



Taxonomic value of anatomical, morphological and palynological characters of *Commicarpus* (Nyctaginaceae) in southern Africa

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Background and aims – The Nyctaginaceae is mainly found in the tropical and subtropical regions of the New World. *Commicarpus* Standl. is the most dominant and diverse genus of the family in southern Africa, and south of the Zambezi River it is distributed throughout the region with a centre of diversity in Namibia. The species are, however, frequently misidentified, calling for the development of a more concise and improved classification system for the region. Nine *Commicarpus* species were investigated, namely *C. chinensis* subsp. *natalensis*, *C. decipiens*, *C. fallacissimus*, *C. fruticosus*, *C. helenae* var. *helenae*, *C. pentandrus*, *C. pilosus*, *C. plumbagineus* and *C. squarrosus*, to identify diagnostic characters that could be useful to distinguish between these infrageneric taxa. Characters are also compared with that of a member of *Boerhavia*, a closely related and morphologically rather similar taxon.

Methods – Flowers were dissected and examined with a stereomicroscope. Pollen grains were acetolyzed and examined with a Scanning Electron Microscope. Leaf and anthocarp material were embedded, stained and examined with a light microscope.

Key results – Morphological features of the flowers and anthocarps provided reliable diagnostic features to distinguish between the species. Anatomical structures and the overall shape and sculpture of the pollen grains were uniform and not differentially diagnostic at infrageneric level.

Conclusions – The structure of the anthocarp and the coriaceous part of the flower are the most valuable diagnostic characters which can be used to distinguish between the different *Commicarpus* species in southern Africa. *Commicarpus* can be distinguished from *Boerhavia* by the flower and anthocarp morphology, and on a micromorphological level based on leaf anatomy.

Key words – Anatomy, anthocarp, *Boerhavia*, *Commicarpus*, diagnostic characters, morphology, Namibia, Nyctaginaceae, palynology, Africa.

INTRODUCTION

The Nyctaginaceae Jussieu is a small flowering plant family of about thirty genera and 400 species (Mabberley 1990). It is commonly known as the Four-O’Clock family, as some neotropical species produce flowers that open in the late afternoon to early evening. The Nyctaginaceae occurs mainly in the tropical and subtropical regions of the New World (Bittrich & Kühn 1993, Jordaan 2000), especially the Americas (Stannard 1988), with some genera extending into temperate regions (Thulin 1994). In the Americas the family has two main regions of distribution i.e. the first being tropical and subtropical South America and the Antilles, and the second, the southwestern United States of America and northern Mexico in North America (Bittrich & Kühn 1993).

In Africa the family is best represented by *Commicarpus* Standl., a genus of about 25 species worldwide with a preference for arid environments (Meikle 1978, Bittrich & Kühn 1993). The genus is distributed throughout the continent, except for the extreme north and south, and the wet, forested areas of the west (Meikle 1978). The arid parts of northeastern tropical Africa and southern Arabia form the centre of diversity for this genus. This is supported by the presence of at least twelve species in Somalia, Ethiopia and adjacent Arabia (Meikle 1978, Thulin 1990). Such an aggregation of species is also true for Namibia, an arid region in southern Africa, which harbors eight species of *Commicarpus* and is probably a second centre of diversity for the genus in Africa.

In southern Africa, being that part of the continent south of the Zambezi River, comprising Botswana, Lesotho, south-

Table 1 – *Commicarpus* taxa of southern Africa and the country distribution of each species.^E: endemic to southern Africa.

<i>Commicarpus</i> species	Country distribution
<i>C. chinensis</i> (L.) Heimerl subsp. <i>natalensis</i> Meikle	Mozambique, South Africa
^E <i>C. decipiens</i> Meikle	Botswana, Namibia
^E <i>C. fallacissimus</i> (Heimerl) Heimerl ex. Oberm., Schweick. & I. Verd.	Botswana, Namibia
^E <i>C. fruticosus</i> Pohnert	Namibia
<i>C. helenae</i> (Roem. & Schult.) Meikle var. <i>helenae</i>	Botswana, Namibia, South Africa
<i>C. pentandrus</i> (Burch.) Heimerl	Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland, Zimbabwe
<i>C. pilosus</i> (Heimerl) Meikle	Botswana, Mozambique, Namibia, South Africa, Zimbabwe
<i>C. plumbagineus</i> (Cav.) Standl. var. <i>plumbagineus</i>	Botswana, Mozambique, Namibia, South Africa, Swaziland, Zimbabwe (and Madagascar)
^E <i>C. squarrosus</i> (Heimerl) Standl.	Botswana, Namibia

ern Mozambique, Namibia, South Africa, Swaziland and Zimbabwe, *Commicarpus* is distributed throughout this region, but is not found in the Mediterranean climate of the Western Cape in South Africa. In southern Africa, the genus is represented by nine species of which four are endemic to the region (table 1) (Germishuizen & Meyer 2003).

Commicarpus forms part of the tribe Nyctagineae, which also include *Boerhavia* L. (Bittrich & Kühn 1993). This tribe is paraphyletic (Douglas & Manos 2007) and *Boerhavia* is polyphyletic, with the genus *Okenia* Schltdl. & Cham. resolving within *Boerhavia*. The genus *Commicarpus* is however, often confused with the closely related and morphologically similar *Boerhavia*, but can be distinguished by its scrambling or climbing habit, flowers with a funnel-shape perianth and an anthocarp that has ten ribs with large, viscid and mucilaginous glands (Meikle 1978, Stannard 1988). *Boerhavia* has a diffuse habit, the flowers are bell-shaped and the anthocarps have 3–4 wings or 5-ribs which are either glabrous or covered in glandular hairs (Codd 1966, Stannard 1988).

However, despite its clear generic circumscription, the different species of *Commicarpus* are frequently confused with each other leading to misidentifications. Meikle (1978) probably best described the problem by stating that all *Commicarpus* species are superficially similar in habit and foliage. This is especially so for dried herbarium specimens which lead to a general misunderstanding of the species concept within the genus. Close inspection of taxa, however, do reveal that each species' habit and morphology is characteristic and open to taxonomic scrutiny. The nine *Commicarpus* species which occur in southern Africa (table 1) were therefore investigated to concisely document diagnostic characters for these taxa based on their morphology, anatomy and palynology. *Boerhavia deserticola* Codd. was included for comparative purpose to emphasise the differences between the two genera in southern Africa.

MATERIAL AND METHODS

Plant material

Leaf, flower and anthocarp material were collected during February and November 2009. Voucher specimens were deposited in the National Herbarium Windhoek, Namibia (WIND), Pretoria National Herbarium, South Africa (PRE), and A.P. Goossens Herbarium, Potchefstroom, South Africa (PUC) (electronic appendix 1).

Morphology

Flower, leaf and anthocarp material were collected in 4% paraformaldehyde. Micrographs of the leaves were taken with a Canon 450D fitted with a 100 mm Sigma macro lens, and micrographs of the flowers and anthocarps with a Nikon DXM 1200F fitted on a Nikon SMZ 1500 stereomicroscope. Leaf and anthocarp measurements (three measurements per specimen) were made from ten herbarium specimens per species. Flowers from three plants per species were dissected. Terminology for the shape of the leaves, anthocarps and flower structure follows Hickey & King (2000).

Palynology

Pollen grains removed from herbarium specimens or flowers preserved in 70% ethanol, were acetolyzed according to the method of Erdtman (1969) with in-house modifications. After acetolysis, the grains were rinsed twice with distilled water and centrifuged at 5000 rpm for 10 min. each. This was followed by dehydration in an ethanol series of 50%, 70% and 96%, with centrifugation at 5000 rpm for 10 min. after each dehydration. The grains were then mounted on specimen stubs and sputter-coated with gold/palladium (Au/Pd) and examined with a FEI Quanta 200 ESEM Scanning Electron Microscope (SEM). Micrographs were taken at 1600 × magnification. Terminology follows Punt et al. (2007).

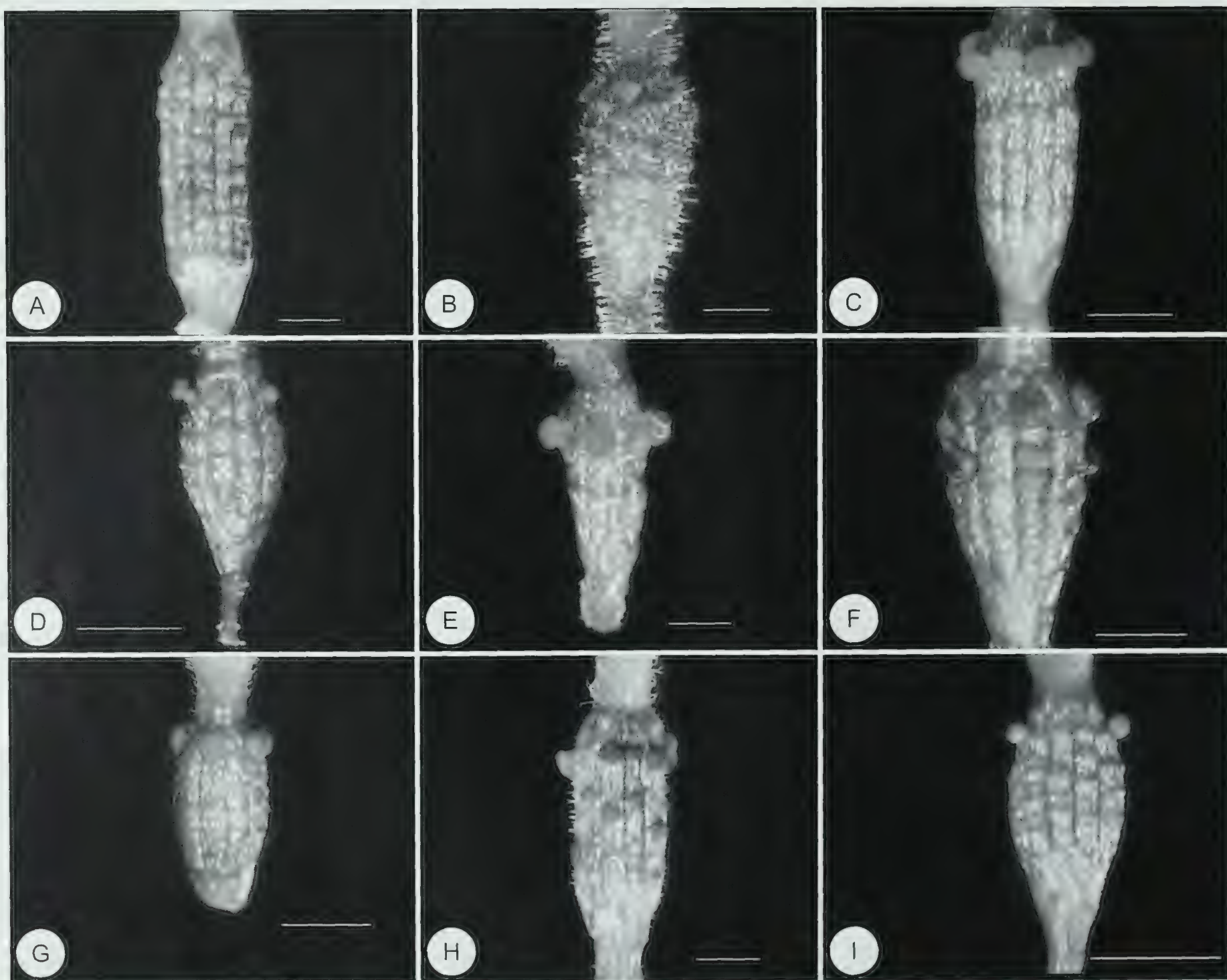


Figure 1 – Micrographs of the shape and arrangement of the glands on the lower part of the flower of the southern African *Commicarpus* species. A, *C. chinensis* subsp. *natalensis*; B, *C. decipiens*; C, *C. fallacissimus*; D, *C. fruticosus*; E, *C. helenae* var. *helenae*; F, *C. pentandrus*; G, *C. pilosus*; H, *C. plumbagineus*; I, *C. squarrosus*. A, C, D, G–I, scale bars = 1 mm; B, E & F, scale bars = 2 mm.

Anatomy

Leaf and anthocarp material were fixed in 4% aqueous para-formaldehyde. Fixed material were then washed three times in 0.05M cacodylate buffer for 15 min each followed by three rinses with distilled water for 15 min each. The material was dehydrated in an ethanol series of 50%, 70%, 90% and twice in 100% ethanol for 15 min each, followed by 15 min in 100% resin (L.R. White™ Wirsam/London Resin Company). This was followed by two consecutive treatments in freshly prepared resin for 60 min each and left over night at 20°C before being imbedded and cured over night at 65°C. A Reichert-Jung microtome was used to make 1 µm sections which were stained with 0.05% aqueous toluidine blue. Micrographs were taken with a Nikon Digital Camera DXM 1200F fitted on a Nikon Eclipse E800 light microscope, and a Nikon Digital Sight Camera fitted on a Nikon Eclipse 80i light microscope.

RESULTS

Habit

The nine *Commicarpus* species are all perennials and their habit can be divided into three growth forms. *C. chinensis* subsp. *natalensis*, *C. decipiens*, *C. helenae* var. *helenae*, *C. pentandrus* and *C. plumbagineus* are herbaceous forbs with stems procumbent, decumbent or scrambling, sometimes upright (electronic appendix 2A). *C. fruticosus* and *C. squarrosus* are sub-shrubs of 0.6–1 m high (electronic appendix 2B) and *C. fallacissimus* and *C. pilosus* have both herbaceous (electronic appendix 2C) and sub-shrub growth forms (electronic appendix 2D). *Boerhavia deserticola*, in contrast, is an upright perennial herb, with numerous 1 m long stems from a basal rosette (electronic appendix 3A).

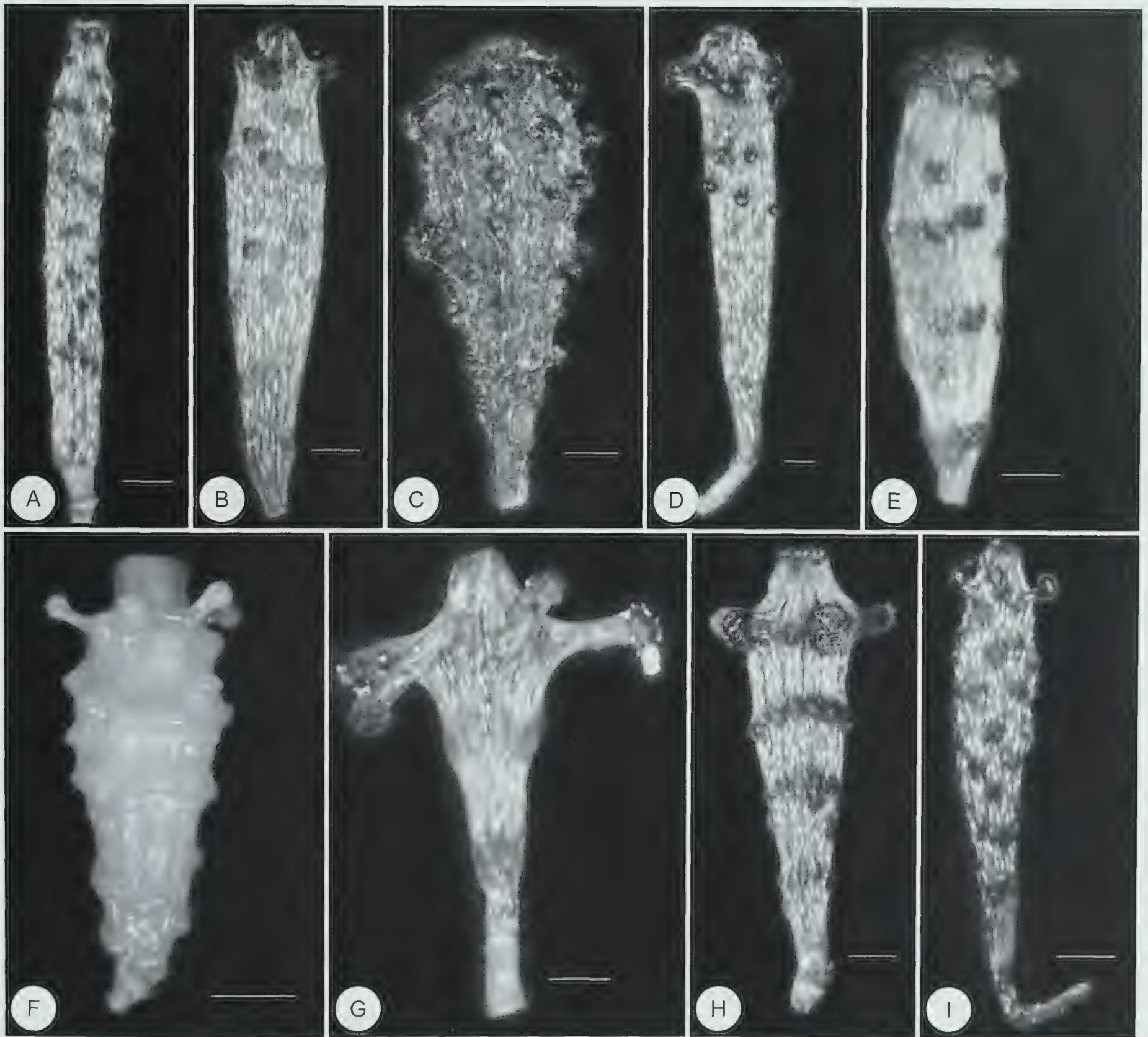


Figure 2 Micrographs of the anthocarps of the southern African *Commicarpus* species. A, *C. chinensis* subsp. *natalensis*; B, *C. fallacissimus*; C, *C. decipiens*; D, *C. plumbagineus*; E, *C. pilosus*; F, *C. fruticosus*; G, *C. helenae* var. *helenae*; H, *C. pentandrus*; I, *C. squarrosus*. Scale bars = 1 mm.

Leaves

The shape of the leaves is variable and can be ovate, deltoid, orbicular, elliptic, oval and lanceolate (electronic appendix 4). The leaves of *C. decipiens* (10–60(–100) × 10–40(–60) mm) (electronic appendix 4B) and *C. plumbagineus* (15–120 × 7–80 mm) (electronic appendix 4H) are the largest and those of *C. fruticosus* (15–33 × 10–27 mm) (electronic appendix 4D), *C. pilosus* (7–50 × 7–50 mm) (electronic appendix 4I) and *C. squarrosus* (10–30 × 10–27 mm) (electronic appendix 4F) are the smallest. The leaves of *B. deserticola* are 15–55 × 5–34 mm, elliptic or oblong (electronic appendix 3B).

Flowers

The flowers of all the members of the *Commicarpus* species are infundibuliform with a distinct lower, coriaceous part and an upper petaloid part (electronic appendix 5). The flowers are 5–14 mm long, with the lower part 2–3 mm long and the upper part 3–11 mm long. The lower, coriaceous part has ten narrow, longitudinal grooves (forming ten ribs) with five to ten prominent glands around the apex and less prominent glands scattered over the surface below (fig. 1). In *C. chinensis* subsp. *natalensis* (fig. 1A) and *C. decipiens* (fig. 1B) the prominent glands around the apex are absent. The upper petaloid part is coloured in white (*C. decipiens* and *C. plumbagineus*), pink (*C. chinensis* subsp. *natalensis* and *C.*

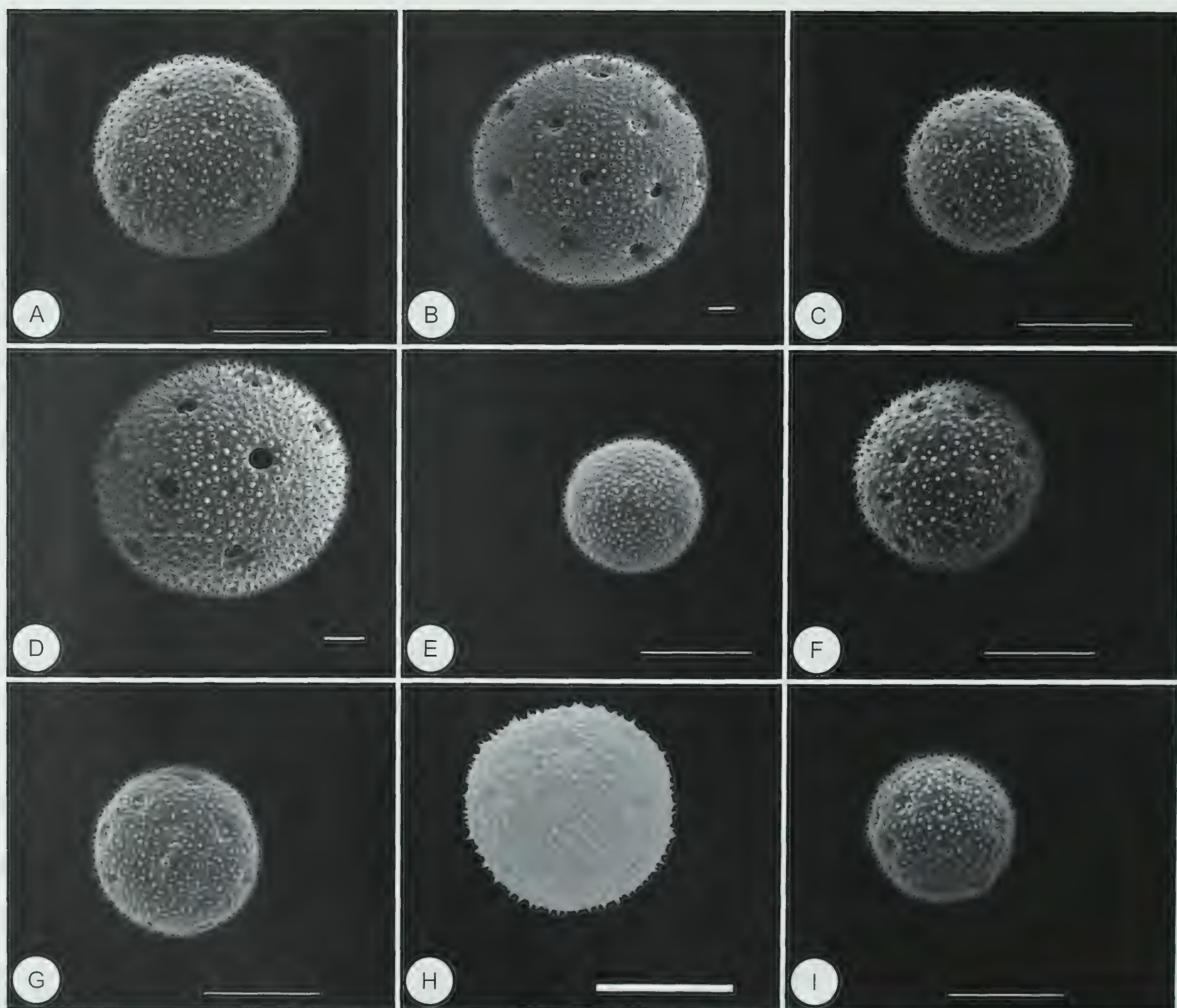


Figure 3 Micrographs of the pollen grains of the southern African *Commicarpus* species: A, *C. chinensis* subsp. *natalensis*; B, *C. decipiens*; C, *C. fallacissimus*; D, *C. fruticosus*; E, *C. helenae* var. *helenae*; F, *C. pentandrus*; G, *C. pilosus*; H, *C. plumbagineus*; I, *C. squarrosus*. A, C, E–I, scale bars = 50 µm, B & D, scale bars = 10 µm

pilosus) or purple (*C. fallacissimus*, *C. fruticosus*, *C. helenae* var. *helenae*, *C. pentandrus* and *C. squarrosus*). The flowers of *B. deserticola* are campanulate and 5 mm long. The lower part is 1 mm and the upper part 4 mm long (electronic appendix 3C). The lower part is clavate, glabrous and with five ribs. The upper part is white or purple.

Anthocarp

The anthocarps are 5–10 × 2–3 mm and the shape is either cylindrical (*C. chinensis* subsp. *natalensis*), fusiform (*C. fallacissimus*, *C. fruticosus*, *C. plumbagineus*, *C. squarrosus*), clavate (*C. decipiens*, *C. helenae* var. *helenae*, *C. pentandrus*) or elliptic clavate (*C. pilosus*) (fig. 2). The apex is surrounded by ten stalked glands (*C. fallacissimus*, *C. plumbagineus*) or five stalked glands alternating with five sessile glands (*C. fruticosus*, *C. helenae* var. *helenae*, *C. pentandrus*, *C. squar-*

rosus) or five stalked glands only (*C. pilosus*). *C. chinensis* subsp. *natalensis* has ten sessile glands around the apex and *C. decipiens* has ten shortly stalked glands around the apex. Sessile wart-like glands are scattered over the surface below the apex (fig 2). The anthocarp of *B. deserticola* is 3–5 × 1–2 mm. It is elliptic-clavate with five conspicuous ribs and the anthocarp is glabrous (electronic appendix 3D).

Pollen

The pollen grains of the *Commicarpus* species (fig. 3) and *B. deserticola* (electronic appendix 3E) are spheroidal and pantoporate with sunken pores which are circular and covered by a pore plate. The tectum is spinulose and tubuliferous. The pollen grains of the *Commicarpus* species are 53–120 µm in diameter, the spinules are 1–5 µm long and the pores 4–8 µm across. *C. chinensis* subsp. *natalensis* (70–120 µm)

(fig 3A), *C. pentandrus* (63–100 µm) (fig 3F) and *C. plumbagineus* (71–105 µm) (fig 3H) have the largest pollen grains and *C. helenae* var. *helenae* (53–71 µm) (fig 3E) and *C. pilosus* (67–77 µm) (fig 3G) have the smallest pollen grains. The pollen grains of *C. fallacissimus* (63–88 µm) (fig 3C) and *C. squarrosus* (61–82 µm) (fig 3I) are in the same size class as that of *B. deserticola* (60–80 µm). The spinules of *B. deserticola* are 2–3 µm long and the pores 5 µm across.

Anatomy

There were no meaningful diagnostic differences in the leaf anatomy of the *Commicarpus* species. In the leaf, the periclinal walls of the guard cells of the stoma are thickened and inner and outer ledges are present. Epidermis cells are large with thin walls (electronic appendix 6A). Crystals of calcium oxalate are present on the periclinal wall of the epidermis cells and are more numerous on the abaxial surface than on the adaxial surface. The mesophyll consists of palisade as well as spongy parenchyma cells which are irregular in shape. Throughout the leaf, idioblasts containing raphides are present in no fixed distribution pattern. The leaf anatomy of *B. deserticola* differs in that the minor veins are surrounded by Kranz anatomy (electronic appendix 6B) whereas the minor veins of *Commicarpus* are surrounded by parenchyma cells. Tannin idioblasts occur along the abaxial surface in *B. deserticola* but are absent in *Commicarpus*.

Similarly, no significant anatomical differences are present in the anthocarps of the *Commicarpus* species. The periclinal wall of the epidermis are thickened and impregnated with calcium oxalate crystals. Bundles of sclerenchyma are present in the ten ribs which are not connected with one another (electronic appendix 6C). The wart-like glands, visible on the outside of the anthocarps, are formed by enlarged ribs with columnar cells. The columnar cells become mucilaginous and a mucoidal is released especially when the anthocarp is wetted. The anthocarp anatomy of *B. deserticola* is only different in that the sclerenchyma is also present in the area between the ribs (electronic appendix 6D).

DISCUSSION

Commicarpus is distinguished from other genera by an infundibuliform flower-shape and a ten-ribbed, fusiform or clavate anthocarp covered with large, viscid, sessile or stipitate glands (Meikle 1978). In southern Africa, *Commicarpus* is frequently confused with *Boerhavia*, but the two genera differ morphologically in that the flowers of *Boerhavia* are smaller than those of *Commicarpus* and are campanulate, and the anthocarps are elliptic-clavate, five-ribbed and without glands (Stannard 1988).

Anthocarp morphology is the character by which most genera have been distinguished within the family (Willson & Spellenberg 1977, Douglas & Manos 2007) and is also a valuable character to distinguish between different species (Bohlin 1988, Turner 1994). The shape of the anthocarp and the arrangement of the stalked glands around the apex, together with the arrangement of the wart-like glands below the apex, is species specific and were used to construct an identification key for the southern African *Commicarpus*

species (Struwig et al. 2011). The arrangement of the glands on the lower, coriaceous part of the flower is also diagnostic as it gives an indication of the arrangement of the glands of the mature anthocarp and is therefore a taxonomic character which can be used to distinguish between non-fruiting specimens with flowers only.

Heimerl (1934) used pollen morphology to divide the Nyctaginaceae into tribes and subtribes and Nowicke (1970) stated that pollen morphology provides a parameter for generic differentiation. The pollen morphology for the former subtribe Nyctaginineae, to which *Commicarpus* belonged, proved to be uniform and of limited value at the generic level (Bogle 1974) and Douglas & Manos (2007) found that pollen morphology did not support tribal and subtribal classification. This claim is supported by the pollen grains of the nine *Commicarpus* species and that of *B. deserticola*, which are uniform in their overall shape and sculpture. It therefore does not provide a useful diagnostic character to differentiate between species (Lindeque et al. 2008).

The anatomy of the leaf and the anthocarp does not provide diagnostic characters to distinguish between the different *Commicarpus* species, but does provide characters to distinguish *Commicarpus* from *Boerhavia*. The minor veins of the leaves of *Boerhavia* are surrounded by Kranz anatomy, which is an indication of the C₄ photosynthetic pathway (Fahn & Cutler 1992), while the minor veins of *Commicarpus* are surrounded by parenchyma cells. Das & Santakumari (1978) investigated *B. diffusa* var. *diffusa* and *B. chinensis* subsp. *chinensis* (synonym for *C. chinensis* subsp. *chinensis*) for the presence of Kranz anatomy and the type of photosynthetic pathway. *B. diffusa* var. *diffusa* had Kranz anatomy and a C₄ photosynthetic pathway, while *C. chinensis* subsp. *chinensis* had no Kranz anatomy and a C₃ photosynthetic pathway. Similarly, Muhaidat et al. (2007) investigated *C. plumbagineus*, *B. coccinea* and *B. dominii* Meikle & Hewson for the presence of Kranz anatomy and only recorded this character for the two *Boerhavia* species.

The anthocarp of *Boerhavia* has five ribs and the sclerenchyma occurs in the rib and the area between the ribs, as was found by Willson & Spellenberg (1977), while in *Commicarpus* the anthocarp has ten ribs with sclerenchyma only occurring in the rib area.

CONCLUSIONS

The habit and leaf shape are diagnostic for the different species, but vegetative characters are pliable and therefore not reliable characters to differentiate between species. The anthocarp and the coriaceous part of the flower provided the most valuable diagnostic characters which can be used to distinguish between the different members of *Commicarpus* in southern Africa. The shape of, and the number and size of the glands on the anthocarp, are diagnostic for each species. Pollen morphology and leaf anatomy cannot be used to distinguish between species although evidence from these sources seems to be useful for higher classifications at the family level.

SUPPLEMENTARY MATERIAL

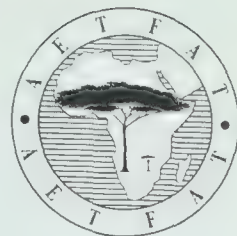
Supplementary data are available in pdf at the Supplementary Data Site of publications from the National Botanic Garden of Belgium (<http://www.nbgpublisher.be> > SBB50 > folder 454) and consist of the following: (1) voucher specimens collected and deposited in three herbaria; (2) growth forms of the southern African *Commicarpus* species; (3) *Boerhavia deserticola*; (4) micrographs of the leaf shape of the southern African *Commicarpus* species; (5) flower of *Commicarpus fallacissimus*; and (6) micrographs of cross sections of leaves and anthocarps of southern African *Commicarpus* species and *Boerhavia deserticola*.

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Manuscript received 28 May 2010; accepted in revised version 8 Feb. 2012.

Communicating Editor: Thomas Haevermans.



Updates on the distribution of Capparaceae and Cleomaceae endemic to Angola

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Background and aims – Both Capparaceae s.s. and Cleomaceae belong to the order Brassicales. Capparaceae include nineteen genera and 439 species, and Cleomaceae thirteen genera and about 238 species. A total of forty species and infra-specific taxa are quoted for these two families from Angola, fifteen of which are considered to be strictly endemic to the country. The main aim of this study is to update the distribution of thirteen of these taxa and to provide estimates of their potential distribution, while assessing which environmental variables most influence it.

Methods – One hundred and fifty herbarium specimens (LISC, LISU, LUAU, COI, K, B) were examined and their location mapped. Using MAXENT models we estimate potential distributions for the seven taxa (through Ecological Niche Model maps) for which, at least five specimens were available.

Key results – Occurrence maps of endemic Capparaceae and Cleomaceae are presented. Two of these taxa (*Boscia gossweileri* and *B. urens*) have ranges extended compared to previous reports. Namibe is the Angolan region where more endemic Capparaceae and Cleomaceae have been found (57 records from 150). Precipitation appears to be the environmental parameter that most influences the distribution of these species, whether either measured as annual precipitation, precipitation in the coolest quarter, or precipitation in the driest quarter.

Conclusions – Most of endemic taxa studied seem to prefer the more arid regions of the country. Comparing potential distribution models with the corresponding known occurrences, *Boscia gossweileri* seems to be the most under-collected. For six of the species studied, more field information is needed before potential distribution can be estimated.

Key words – Angola, endemism, Capparaceae, Cleomaceae, occurrence, potential distribution models.

INTRODUCTION

Understanding the distribution of endemic plants and of their ecological requirements is a necessary step to propose conservation measures and assess their efficiency. This is especially relevant in sub-Saharan African countries, where several centres with high rates of endemism have been identified (Lovett et al. 2000, Linder 2001, Küper et al. 2004) and habitat preservation is in many cases urgent.

Several authors have mentioned the high rate of endemism of Angolan flora (Exell & Gonçalves 1973, Linder 2001, Moreira et al. 2006, Figueiredo et al. 2009), which appears to be the second richest in southern and south-tropical Af-

rica, after South Africa (Figueiredo et al. 2009), with 14.80% species endemism, down from the 27.3% rate indicated by Exell & Gonçalves (1973). Despite these preliminary estimates, studies in specific groups of endemics are lacking to evaluate the distribution of restricted-range species in the country. Such studies may help to clarify the disparity among published figures of endemism as well as on centres of endemism and high species richness.

Two main centres of endemism have been previously identified within Angola: one in the east, which Linder (2001) suggests represents the western end of the Zambezi-Congo watershed centre, and the other in the south-west, which he termed the 'Huilla centre'. The latter was also

referred to by Exell & Gonçalves (1973), who considered it to be “the main centre of endemism in the country, and one of the most important in tropical Africa”. Maggs et al. (1998) also mention the area north to the border with Namibia, which is included in the Kaokoveld centre of endemism (Maggs et al. 1998, Craven & Vorster 2006, Craven 2009b), as having extremely high species richness and endemism. Some of the species mapped in this work are described by Craven (2009b) as endemic to the Kaokoveld, although their occurrence has not yet been reported in Namibia. Both Exell & Gonçalves (1973) and Brenan (1978) indicate that endemism is indeed high throughout Angola, the latter presenting a figure of 1260 endemic species as an estimate based on extrapolation from a sample.

Capparaceae and Cleomaceae, a pair of closely related families, are estimated to include 439 and 238 species, respectively (APG III 2009). A total of 15 taxa belonging to these families are considered endemic to Angola (Figueiredo & Smith 2008). The only study to date on Capparaceae from Angola was that in the first volume of the incomplete work *Conspectus Florae Angolensis* (Exell & Mendonça 1937), which was already considered as “considerably out-of-date” by Brenan in 1978. Two of the species considered in the present work had not even been described in 1937 – *Cadaba benguellensis* Mendes (Mendes 1967) and *Cleome rubelloides* Kers (Kers 1970). Gathering and mapping the known collections was therefore an important step to improving knowledge of these species.

When dealing with data of heterogeneous quality regarding the description of localities such as herbarium data, and in the absence of either systematic sampling or reliable information on species absence, spatial distribution models based on presence-only information have recently been shown to offer a robust tool to estimate species distribution (Braunisch & Suchant 2010) that has played an increasing role in species conservation and has shown a strong performance (Hernandez et al. 2006, Rebelo & Jones 2010). Using such methods to model potential distribution of Capparaceae and Cleomaceae contributes to the study of poorly known species in both families. Therefore, we aim to update the known distribution of selected taxa in these groups using available herbaria collections, and to develop models that predict their potential distribution, highlighting the environmental variables that might best explain those results. We also briefly comment on the distribution of Capparaceae and Cleomaceae collections with respect to the centres of species richness previously identified in Angola.

MATERIAL AND METHODS

Study area

According to Exell & Gonçalves (1973) and Huntley & Matos (1994) four main physiographic components characterize Angola (South West Africa): an arid coastal plain from the Atlantic seaboard to approximately 200 m above sea level; a narrow steep escarpment, between 200 and 1000 m; an interior plateau, occupying nearly 80% of the country, from 1000 to 1600 m; and a mountain belt rising above the plateau, with altitudes that reach 2620 m (fig. 1).

Annual Precipitation in the country decreases sharply from the northeast, where the rainy season dominates the dry season, to the southwest, where the littoral south is more arid (electronic appendix 1). The highest annual mean temperatures occur in the coastal belt, but are lower than one might expect in the southwest (electronic appendix 2) due to the influence of the Benguela cold current. The climate of Angola is for the most part dry tropical.

Regarding land cover (electronic appendix 3), a large region of forest ranges from northeastern to central Angola, which includes deciduous forests (also referred as miombo woodland), interspaced with mosaics of forest or shrubland and grassland (FAO GeoNetwork 2010a). This mosaic merges with more open vegetation, composed of grasslands and shrublands, covering the western and southern regions. In the Namib Desert region and from the south of Benguela, southwest Angola, the vegetation is mainly sparse and dwarf in stature.

Taxa studied

A definition of endemic species was used that considers the political borders of Angola. We believe that country endemism is important for the future implementation of conservation policies, as the conservation of endemic species relies on national environmental policies (Craven & Vorster 2006, Mills 2010). Species whose potential distribution indicates a high likelihood in areas of border with an adjacent country, could be referred as near-endemics. However, without evidence of their occurrence outside Angola, we refer them here as endemics.

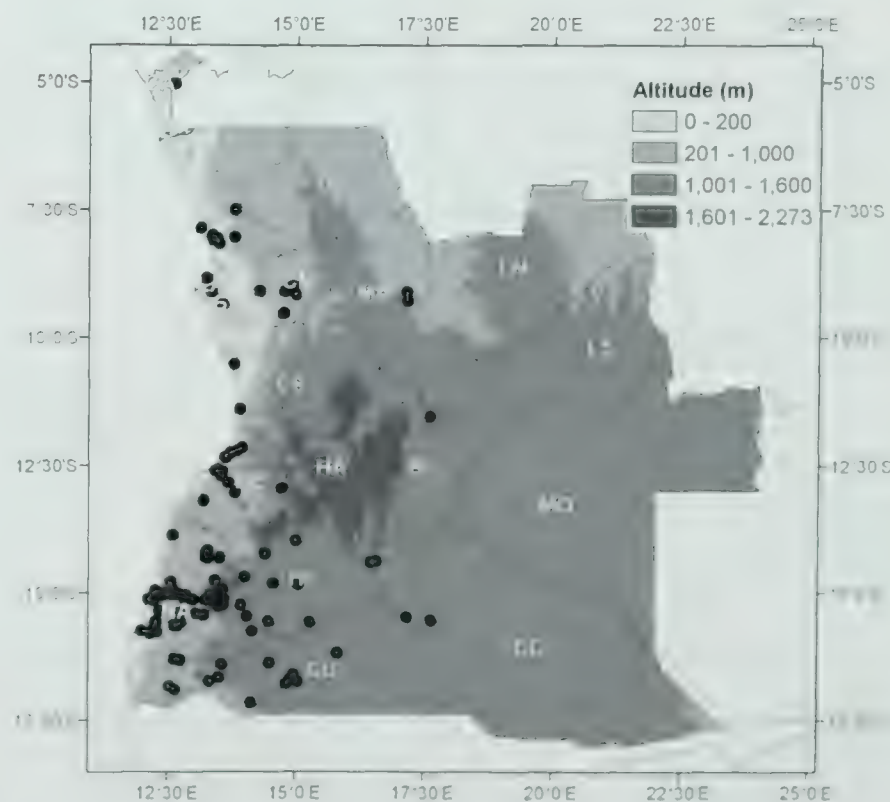


Figure 1 – Digital elevation model of Angola. Data on altitude from Jarvis et al. (2008). Black dots correspond to the mapped occurrences of all the Capparaceae and Cleomaceae studied. CA - Cabinda; ZA - Zaire; UI - Uíge; LA - Luanda; BO - Bengo; CN - Cuanza Norte; MA - Malange; LN - Lunda Norte; CS - Cuanza Sul; LS - Lunda Sul; BE - Benguela; HA - Huambo; BI - Bié; MO - Moxico; NA - Namibe; HI - Huila; CU - Cunene; CC - Cuando Cubango.

Thirteen endemic taxa of Capparaceae and Cleomaceae were studied: *Boscia gossweileri* Exell, *B. pestalozziana* Gilg, *B. polyantha* Gilg, *B. urens* Welw. ex Oliv., *Cadaba benguellensis*, *Euadenia brevipetala* Exell, *Ritchiea agelaeifolia* Gilg, *R. noldeae* Exell & Mendonça from Capparaceae; and *Cleome gossweileri* Exell, *C. kermesina* Kers ex Gilg & Gilg-Ben. var. *kermesina*, *C. kermesina* var. *plebeia* Kers, *C. mossamedensis* Exell & Mendonça, *C. rubelloides* from Cleomaceae. For the remaining two endemic taxa, *Ritchiea carrissoi* Exell & Mendonça and *Ritchiea mayumbensis* Exell, no available collections had detailed enough distributional information to allow their study.

Specimens and data sources

Specimens housed at six herbaria (B, COI, K, LISC, LISU, LUAU) were examined, (acronyms following Holmgren et al. 1990). All accessions of the thirteen endemic taxa studied, totalling 150 vouchers, were taxonomically revised and previous determinations were re-evaluated.

Floras used to study the herbarium material are cited by the following abbreviations: *Conspectus Florae Angolensis* – CFA (Exell & Mendonça 1937, 1951); *Flora Zambesiaca* – FZ (Wild 1960); *Flora of Tropical Africa* – FTA (Oliver 1868); *Flora of Tropical East Africa* – FTEA (Elders et al. 1964); *Flora of West Tropical Africa* – FWTA (Hutchinson & Dalziel 1954); and *Prodromus einer Flora von Südwestafrika* – FSWA (von Merxmüller 1966).

We also consulted several electronic resources, the African Plants Database (2010), Tropicos (2010), and the International Plant Names Index (2010), to check nomenclature issues and/or synonymy. Type material not physically available to us was accessed through JSTOR Plant Science (2010). Endemicity was checked against published floras of the neighbouring countries: Namibia (Craven 2009a), Zambia (Phiri 2005) and Democratic Republic of the Congo (Hauman & Wilczek 1951), as well as *Flora Zambesiaca* (Wild 1960). For some species of Capparidaceae, the treatment in the *Flore du Gabon* was also consulted (Kers 1987).

Georeferencing and distribution modeling

All specimens were georeferenced using the guidelines from Chapman & Wiecek (2006), based on the locality descriptions on specimens labels. In cases where the description was not adequate to map the collections but other sources of original information from the collectors (either field books, travel itineraries or correspondence) were available at LISC, they were used to determine where the specimens have been collected. Specimens whose associated geographic data did not fit the criteria of Chapman & Wiecek were excluded from the study. In all, 150 specimens were mapped.

All localities were initially submitted to Biogeomancer Workbench (Biogeomancer Working Group 2009), or when this gazetteer contained no corresponding records, localities were alternatively sent to GEOLocate (2010). Coordinates were subsequently adjusted and finalized by placing points on the military maps of Angola, at scale of 1:100,000 (Ministério do Ultramar 1951–1969). For all sites, the value of uncertainty was determined using the protocol indicated by

Chapman & Wiecek (2006). Specimen occurrences were mapped using ArcGIS 10.0 (ESRI 2010).

Environmental datasets

The environmental dataset included the 19 Bioclim variables, at 2.5 arcminute resolution, from the Worldclim dataset (Hijmans et al. 2005). The layer for altitude was taken from the same dataset. Data on land cover and soil, used as categorical variables, are simplified from the Globcover regional dataset (FAO GeoNetwork 2010a, 2010b), available online from FAO Geonetwork.

Ecological niche modelling

Potential distribution of the taxa studied was carried out using presence-only modelling techniques, using Maxent (Phillips et al. 2006). Only species with a minimum of 5 collections were considered adequately sampled to predict potential distribution. This was done considering the spatial representativeness of the samples in relation to the model spatial domain and the set of environmental features relevant for the model of each species. Redundant locations for a given species were excluded. Colinearity of environmental variables in Maxent models was avoided by running an initial jackknife analysis, retaining for the model the six environmental variables with the highest contributions. Among these six, redundancy between variables was minimized through user selection. To assess the predictive performance of the models, we used the area under the Receiver Operating Characteristic curve (AUC) as a statistic to test performance of species distribution models (Milne et al. 2006, Sérgio et al. 2007).

RESULTS

Distribution

Specimen occurrences for the 13 taxa studied are shown in figs. 2A–E. Some collections cited for several species are reported here for the first time: 9 of the 15 collections of *Boscia gossweileri*, located in the provinces of Huíla (6), Malange (1), Namibe (1) and Cunene (1); 1 of the 19 collections of *B. pestalozziana*, from Namibe; 14 of the 24 specimens of *B. polyantha*, in Namibe (11), Huíla (2) and Cunene (1); 14 of 28 collections of *B. urens*, from Bengo (4), Cuanza Norte (2), Cuanza Sul (2), Luanda (2), Benguela (2) and Namibe (2); and 5 of the 23 specimens of *Cleome mossamedensis*, all from Namibe. For *Euadenia brevipetala* Exell, previously known only from the type (Flora of Angola Online 2010, African Plants Database 2010), no new occurrences were recorded (fig. 2E).

For the spatial distribution modeling, 7 models were plotted for the seven species with a minimum of 5 collections using ArcGIS 10.0, after model building with Maxent (Phillips et al. 2006), as shown in fig. 3 for Capparaceae and fig. 4 for Cleomaceae. For all models, AUC values were higher than 0.9 (table 1), demonstrating a good performance.

Boscia gossweileri (fig. 3A) seems to have the most heterogeneous habitat preferences, while *B. urens* (fig. 3D) and

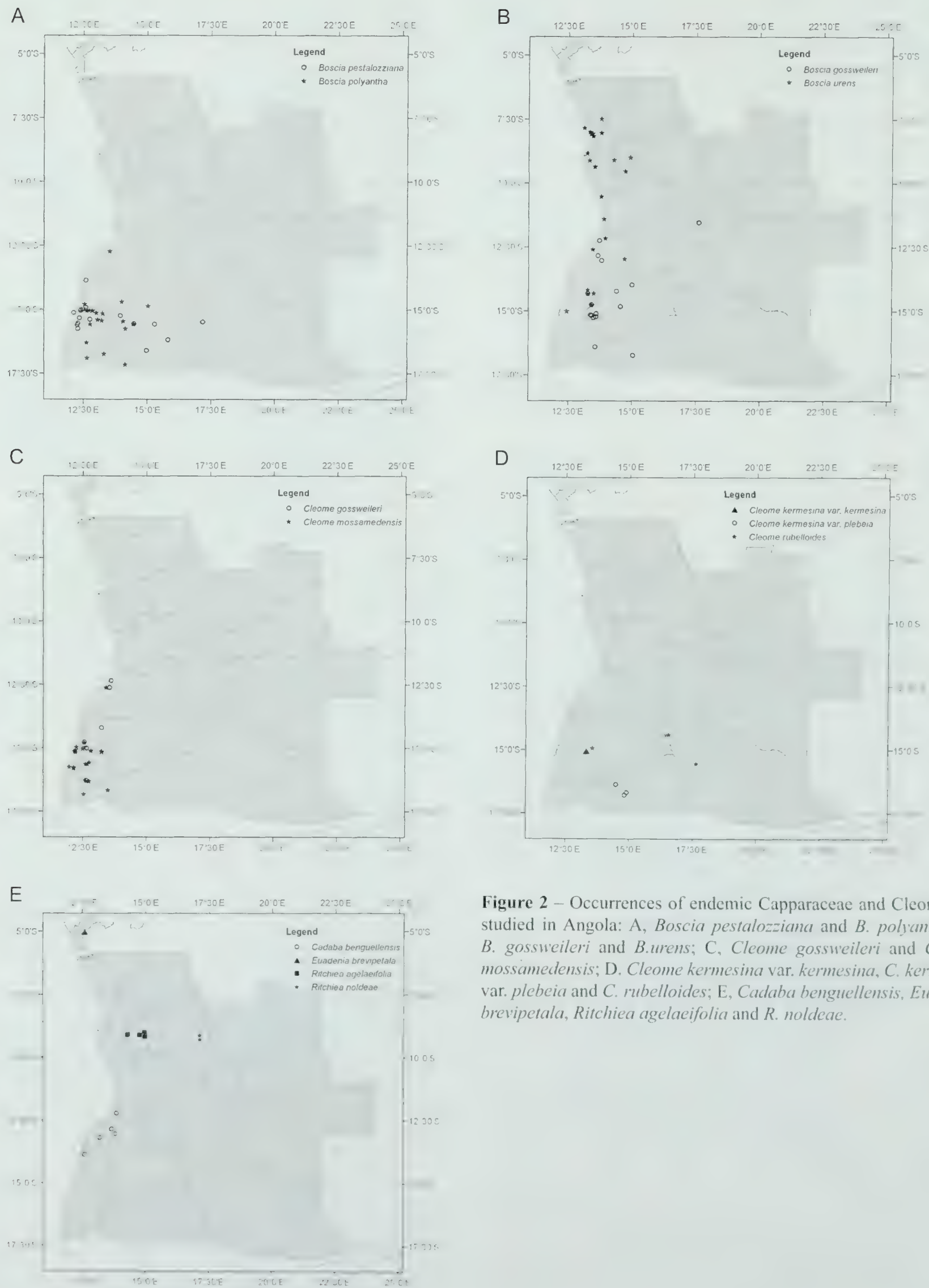


Figure 2 – Occurrences of endemic Capparaceae and Cleomaceae studied in Angola: A, *Boscia pestalozziana* and *B. polyantha*; B, *B. gossweileri* and *B. urens*; C, *Cleome gossweileri* and *Cleome mossamedensis*; D, *Cleome kermesina* var. *kermesina*, *C. kermesina* var. *plebeia* and *C. rubelloides*; E, *Cadaba benguellensis*, *Euadenia brevipedata*, *Ritchiea agelaefolia* and *R. noldeae*.

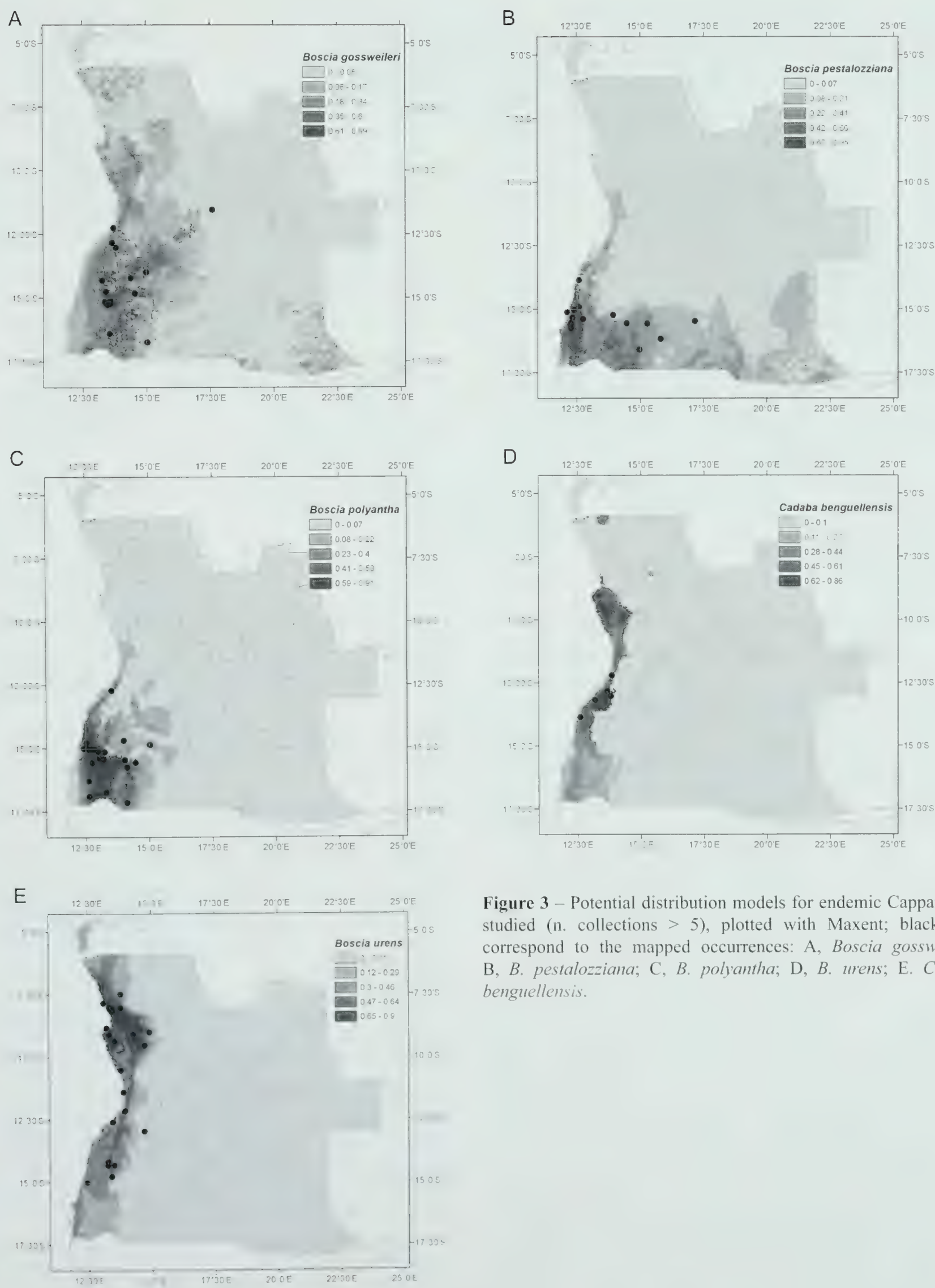


Figure 3 – Potential distribution models for endemic Capparaceae studied (n. collections > 5), plotted with Maxent; black dots correspond to the mapped occurrences: A, *Boscia gossweileri*; B, *B. pestalozziana*; C, *B. polyantha*; D, *B. urens*; E. *Cadaba benguellensis*.

Table 1 · Environmental variables and corresponding percentage of contribution (in parenthesis) used to model the potential distribution of the listed taxa.

The Area Under the Curve (AUC) parameter for each of the models is also presented.
AT - Annual Mean Temperature, MDR - Mean Diurnal Range, MTCM - Min Temperature of Coldest Month, TAR - Temperature Annual Range, AP - Annual Precipitation, PWM - Precipitation of Wettest Month, PS - Precipitation Seasonality, PWtQ - Precipitation of Wettest Quarter, PDQ - Precipitation of Driest Quarter, PWmQ - Precipitation of Warmest Quarter, PCQ - Precipitation of Coldest Quarter, LC - Land Cover, DSOIL - Dominant Soils.

Species	number of samples	AUC	Environmental Variables
<i>Boscia gossweileri</i>	16	0.94	LC(29), AT(25), PDQ(21), TAR(15), AP(8), MDR(2)
<i>Boscia pestalozziana</i>	15	0.96	PCQ(37), LC(28), PWtQ(21), DSOIL(5), AP(5), TAR(4)
<i>Boscia polyantha</i>	21	0.98	DSOIL(45), PCQ(22), TAR(16), PWmQ(8), PDQ(5), LC(3)
<i>Boscia urens</i>	23	0.96	TAR(37), ALT(18), DSOIL(16), PS(15), MDR(9), MDR(7)
<i>Cadaba benguellensis</i>	5	0.99	PDQ(40), TAR(33), DSOIL(17), PWM(5), PCQ(4), LC(1)
<i>Cleome gossweileri</i>	6	0.99	DSOIL(29), TAR(25), LC(17), AP(11), MDR(10), PS(8)
<i>Cleome mossamedensis</i>	20	0.99	AP(57), TAR(12), PDQ(9), PWtQ(9), ALT(6), DSOIL(6)

Cadaba benguellensis (fig. 3E) show a high probability of occurrence in the sublittoral zone, extending to the north of Benguela. Apart from these taxa, the remaining distribution models show higher probabilities of occurrence in the desert region in the southwest of the country.

Environmental variables and potential distribution

The variables that most contribute to the distribution models presented here are shown in table 1. Temperature and precipitation are the best predictors of distribution for most species, whether calculated as variation ranges, extreme values or average values (temperature). Temperature is the most commonly represented, present in six of the seven taxa modeled (absent only in *Boscia pestalozziana*). Variables related to precipitation are the second most represented, either expressed annually or as the coldest/ dryer quarter. The variable “dominant soils” seems to contribute significantly to explaining the distribution of four taxa, “land cover” for three taxa, and “altitude” to a single taxon, *Boscia urens*.

DISCUSSION

An analysis of the mapped occurrences (fig. 2) shows that most species were collected in the southwestern part of the country, five of which having been found mainly in that region: *Boscia pestalozziana* and *B. polyantha* (fig. 2A), *Cleome mossamedensis* and *C. gossweileri* (fig. 2C) and *Cadaba benguellensis* (fig. 2E), although this last taxon has a high probability of occurrence extending up to Luanda. On the other hand, the species of *Euadenia* and *Ritchiea* are only represented in the north and centre-north of the country (fig. 2E): *Euadenia* mapped only in the Cabinda region, in the area of Maiombe forest, and *Ritchiea* in the provinces of Malange and Cuanza Norte, probably associated to areas of particular elevations in those regions. Regarding *Boscia pestalozziana* and *B. polyantha*, the mapped occurrences confirm the ecological preferences previously mentioned for both species, i.e. sandy and dry places for the first species

(Exell & Mendonça 1937, African Plants Database 2010) and xerophytic scrub and open areas for the second (Costa et al. 2009, Exell & Mendonça 1937).

Besides being well represented in the southwest desert region, endemic Capparaceae and Cleomaceae are also numerous in the region adjacent to the narrow steep escarpment corresponding to the boundary between Namibe and Huíla (fig. 1), identified by White (1983) as a fringe of the phytocorion he referred to as the “Kalahari-Highveld regional transition zone”. Locally called *Fenda da Tundavala* and surrounded by the *Serra da Chela* mountain, this region abruptly separates the Namibe desert (Namibe) from the interior plateau (Huíla). It is very rich in endemic species in general (Exell & Gonçalves 1973) apparently due to its extreme ecological conditions. An explanation for this richness in endemics could be the fact that this region has served as a refuge where ecological conditions remained stable during periods of climatic fluctuation (Exell & Gonçalves 1973), enabling the persistence of species that were unable to survive elsewhere due to unsuitable conditions. This is consistent with Linder’s (2001) hypothesis that regions with high levels of endemism reflect refuges from climate and vegetation change.

Although our study deals with two small families comprising relatively few species, and does not seek to assess global endemism levels or centres of endemism, our results are nevertheless consistent with the notion that the southwestern region of Angola has a high presence of endemic species. The same pattern has been observed in Leguminosae (Soares et al. 2007), the family with the highest level of endemism in the country (Figueiredo et al. 2009). This reinforces the richness of Kaokoveld centre of endemism (Craven & Vorster 2006, Craven 2009b), which includes the southwestern region of Angola. On the other hand, the region that Exell & Gonçalves (1973) refer to as the main centre of endemism in the country, ‘Benguela-Huíla-Bié’, which is broader than Kaokoveld and includes its northern part, has a lower predicted number of occurrences of endemic species. The same is true if considering the Huíla region, identified

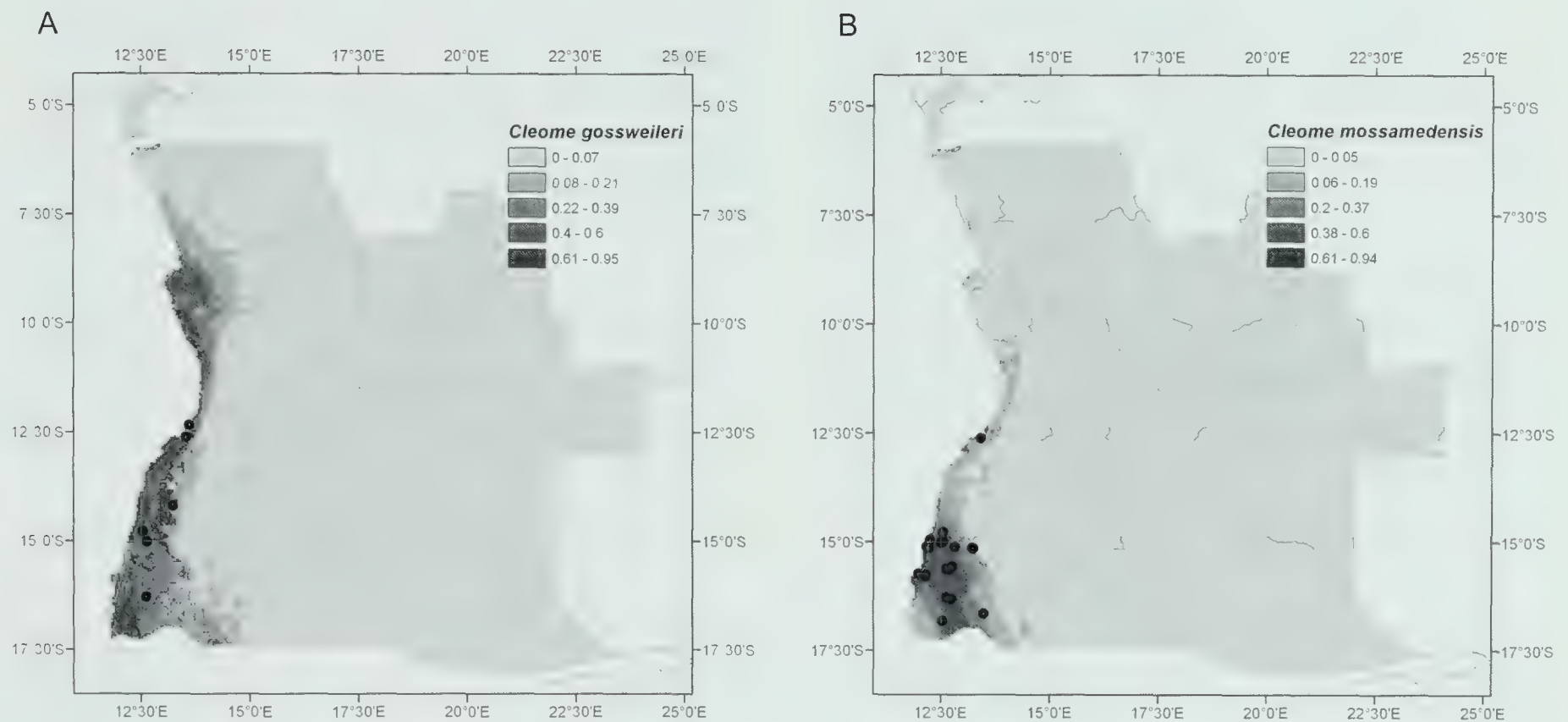


Figure 4 – Potential distribution models for endemic Cleomaceae studied (n. collections > 5), plotted with Maxent; black dots correspond to the mapped occurrences: A, *Cleome gossweileri*; B, *C. mossamedensis*.

by Linder (2001) as a centre of endemism. The other centre of endemism identified in the country by the same author (Linder 2001), as a continuation of the Zambezi-Congo watershed centre and including part of Moxico and Lunda Sul, does not seem to have predicted presence for most of the thirteen analysed taxa, according to the distribution models. Our results also seem to corroborate the idea proposed for Namibia by Craven & Vorster (2006) that hot deserts usually have a high occurrence of endemics.

Maps showing probability of occurrence (fig. 3) significantly extend the potential range for some of the species modeled, such as *Boscia gossweileri* and *B. pestalozziana*. For others, the area is extended only latitudinally but remains restricted to the coastal region, as is the case for *B. urens*, *Cadaba benguellensis* and *Cleome gossweileri*. These results also suggest that there are regions where the occurrence of some species is predicted but, as far as we know, they have not yet been recorded. This information can help inform which areas need to be more explored, for endemic Capparaceae and Cleomaceae, being potentially relevant for planning a future assessment of threat status (Sérgio et al. 2007). Among the 13 taxa studied, the one that seems to have been most under-collected is *Boscia gossweileri*, which has a large potential area of occurrence when compared to the range of the known collections, with potentially suitable habitat extending to the north and southeast. On the other hand, the taxon with an apparently more restricted area of occurrence, considering the relatively high number of assessments when compared with the remaining taxa, is *Cleome mossamedensis*.

The areas of potential occurrence of some of the taxa studied would clearly extend into parts of Namibia, if no mask had been applied to the Maxent models corresponding to the border between the two countries, allowing us to ex-

plore the full potential range of these species. The species that might be present in northern Namibia include *Boscia gossweileri*, *B. pestalozziana* and *B. polyantha*, which might more correctly be referred to as near-endemics to Angola, as they have been mentioned as occurring in the Kaokoveld centre of endemism (Craven 2009a) whose potential distribution is adjacent to the frontier with Namibia. We have, however, chosen to adopt a conservation-based approach to describing the status of these taxa, according to which their preservation depends on the country in which most of their presence occurs.

Data on the distribution of Capparaceae and Cleomaceae will no doubt be improved as progress is made on documenting the floras of other African countries, and as additional collecting is done, including within Angola. This can be deduced from the fact that several taxa are predicted to occur in some regions of the country in which they have not yet been recorded. Further field work and taxonomic studies, either in neighbouring countries and in Angola, may also enlarge the distribution range of the species studied, and may bring new species to the country's flora.

SUPPLEMENTARY MATERIAL

Supplementary data are available in pdf at the Supplementary Data Site of publications from the National Botanic Garden of Belgium (<http://www.nbgpublisher.be>), folder 471, and consist of the following: (1) spatial distribution of Annual Mean Precipitation in Angola; (2) spatial distribution of Annual Mean Temperature in Angola; (3) land cover map of Angola, from Globcover Regional (FAO GeoNetwork 2010a); (4) exsiccata.

ACKNOWLEDGMENTS

We thank FCT (the Portuguese Foundation for Science and Technology) for funding this work, developed in the scope of IMBAMBA project (reference PTDC/BIA-QOR/66702/2006). We also acknowledge Estrela Figueiredo for having initiated this project.

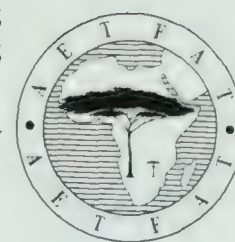
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Manuscript received 5 Jul. 2010; accepted in revised version 23 Feb. 2012.

Communicating Editor: Porter P. Lowry II.



The Cyperaceae in Madagascar show increased species richness in upland forest and wetland habitats

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Background and aims – Madagascar is a biodiversity hotspot with a high level of plant endemism. However, not all lineages of plants are equally represented and the highest diversity occurs in forest lineages. Cyperaceae frequently occur in grasslands and wetlands in Africa, and the tribe Hypolytreae and *Carex* subgenus *Vigneastra* are among the few predominantly forest lineages. We study the Cyperaceae of Madagascar to discover what lineages are represented (genera/tribes), to determine their unique habitats and key functional traits and to investigate patterns of species richness.

Methods – The World Checklist of Monocotyledons was queried for Cyperaceae occurring in Madagascar. The global distribution of these species was investigated to identify endemic taxa and to evaluate other botanical countries where widespread species occur. Data on life form, habitat and photosynthetic type were scored from literature and personal observations.

Key results – Madagascar has 321 species of Cyperaceae in 33 genera, representing all major clades of the family. The predominantly tropical Cypereae clade composes about half of the sedge flora, of which *Cyperus* represents about a third of the species in Madagascar. The Cariceae, a predominantly northern hemisphere temperate clade, is unusually highly represented and composes 10% of the sedge flora, occurring mostly in the highlands. In Madagascar, 55 species (17% of flora, mainly *Carex* and *Cyperus*) occur in forests and all are C₃ perennials. *Bulbostylis* and *Pycneus*, exclusively C₄ taxa with high proportion of annuals compared to C₃ genera in Madagascar, occur outside forests in seasonal or permanent wetlands. Endemism among the sedge flora is 37% (121 species), a third of which (42 species) occur in forests, mostly in the Central and Eastern highlands.

Conclusion – Cyperaceae are among top ten species richest angiosperm families in Madagascar. When compared with other botanical countries, Madagascar has the second highest endemism level, second to the Cape Provinces. The sedge flora assembly has involved long distance dispersal(s) coupled with Neogene radiation in upland humid forests and open wetland habitats.

Key words – Biogeography, conservation, Cyperaceae, C₄ photosynthesis, functional traits, species richness.

INTRODUCTION

Madagascar is one of the hottest biodiversity hotspots (Myers et al. 2000, Brummitt & Lughadha 2003) with levels of endemism as high as 90% for many groups of plants and animals (Goodman & Benstead 2003, Wilme et al. 2006, Vences et al. 2009). The island, measuring about 594,000 km², has an estimated 14,000 species of higher plants (Goodman & Ben-

stead 2005, Phillipson et al. 2006). Among the larger vascular plant families, the highest species richness and endemism are found in Orchidaceae (871 species/96% endemic, World Checklist of Monocotyledons 2010), Euphorbiaceae (700, mostly endemic, Hoffmann & McPherson 2003), Rubiaceae (650/98% endemic, Davis & Bridson 2003), Leguminosae (573/80% endemic, Labat & Moat 2003) and Melastomataceae (321/99% endemic, Almeda 2003). A number of large

angiosperm families such as Asteraceae, Cyperaceae and Poaceae, which are predominantly herbaceous, do not have high levels of endemism, thereby raising questions on what dictates patterns of species richness in Madagascar.

The high level of species richness and endemism is partially due to the geological history of the island. The Malagasy tectonic plate separated from Africa about 165 million years ago (Wells 2003), long before the origin of the extant flora and fauna. The African continent is the closest large land mass, c. 400 km away. Additionally, a number of smaller volcanic islands of varying ages and sizes occur in the surrounding Indian Ocean. The island reached its current latitude only recently and there is overwhelming evidence supporting the Cenozoic origin of Malagasy clades whose sister taxa occur in mainland Africa (Yoder & Nowak 2006). Prior to the Oligocene the southern tip was below 30°S and Madagascar experienced drier conditions (Wells 2003). It is therefore hypothesized that the subarid spiny scrub biome dominated Madagascar and that the other biomes (evergreen and deciduous forests, montane types and grasslands) have evolved subsequently (Wells 2003).

Madagascar's current mostly tropical location accompanied by varied climate, topography and geology, provides a large variety of potential habitats for terrestrial organisms. Elevation and climate (annual rainfall and temperature) determine contemporary boundaries of biomes or bioclimatic regions (Moat & Smith 2007) – the wetter eastern coast has evergreen forests, the central highlands have grasslands and deciduous woodlands, the drier and hotter western slopes and lowlands have deciduous forests, whereas the arid south western areas have spiny scrub (Cornet 1974, Wells 2003). Different functional traits are characteristic of adaption to the various biomes; for example, succulence and specialized photosynthetic systems (C_4 and CAM photosynthesis) are prevalent in the subarid spiny scrub flora.

A large number of the endemic vascular plant lineages (e.g. within the Rubiaceae, and Melastomataceae, Almeda 2003) have diversified in forests located in the evergreen humid and deciduous forests. Diversification in forest habitats involves competition for space, water and light; hence plant lineages with favoured traits (e.g. growing into shrubs/trees, epiphytism, C_3 photosynthesis) dominate, whereas lineages adapted to open canopy habitats would be excluded. Among the graminoids, wetter, forest habitats are dominated by C_3 perennial taxa such as bamboos (Dransfield 2003), whereas drier/arid habitats would be expected to have more C_4 , hemicryptophytic and/or annual taxa.

The Cyperaceae is a family of monocotyledons that is most diverse in open habitats. The family comprises c. 5,400 species in 106 genera (Govaerts et al. 2007), classified into sixteen tribes and two subfamilies (Goetghebeur 1998, Muasya et al. 2009). Subfamily Mapanioideae (c. 170 species) comprises tribes Hypolytreae and Chrysitricheae. The former is mostly restricted to tropical forests whereas the latter occurs in southern hemisphere heathlands (Muasya et al. unpubl.). Subfamily Cyperoideae comprises about 97% of the family, with notable diversity in northern temperate (Cariceae, c. 1,900 species), southern temperate (Schoeneae, c. 260 species) and tropical regions (Cypereae, c. 1,100 spe-

cies; Abildgaardieae, c. 520; Rhynchosporae, c. 380; Eleocharideae, 260, and Sclerieae, c. 260). In tropical Africa, the family has high species richness among tribes Cypereae and Abildgaardieae in the savannas, exhibiting C_4 photosynthesis, an annual life form, poikilohydry and other adaptations. In Madagascar, the Cyperaceae is the richest wetland plant family, with about 142 wetland species of which 51 are endemic (Andrianasetra Ranarijaona 2003).

Modern lineages of Cyperaceae evolved in the Tertiary (Besnard et al. 2009). Therefore the Cyperaceae in Madagascar have either dispersed into or evolved *in situ* from Gondwanan ancestors or from ancestors that colonized the islands during the Cenozoic. This study explores Cyperaceae diversity: (1) to investigate patterns of species richness and endemism; (2) to identify key functional traits in lineages that have diversified in Madagascar and their corresponding habitats.

MATERIALS AND METHODS

The World Checklist of Monocotyledons (2010) was queried for Cyperaceae growing in Madagascar (electronic appendix 1). This peer-reviewed database of names of accepted taxa provides global distributions of species in botanical countries as recognized by the Taxonomic Databases Working Group (TDWG; Brummitt et al. 2001). Occurrence of Cyperaceae species in Madagascar and other botanical countries, where relevant, was plotted using ArcView GIS Version 3.1. For each species, the habitat (forest/open) and life form (therophyte or not) were scored from literature (e.g. Chermezon, 1937) and supplemented with field observations. The photosynthetic type (C_3/C_4) was based on literature (e.g. Bruhl & Wilson 2007) and supplemented with recent studies (Laridon et al. 2011).

RESULTS

Madagascar has 321 species of Cyperaceae in 33 genera, representing thirteen tribes and all subfamilies (table 1, electronic appendix 1). The largest tribes are Cypereae (49% of the sedge flora), Abildgaardieae (12%) and Cariceae (11%). Four tribes (Bisboeckelereae, Chrysitricheae, Cladieae, Triplepideae) have a single species in Madagascar. *Cyperus* is the largest genus, composing about 31% of the flora, followed by *Carex* (10%). Thirteen genera have a single species (40% of all genera or 4% of all species), one of which (*Trichoschoenus*) is a monotypic endemic genus. A number of the genera with a single species in Madagascar are wetland plants with pantropical (e.g. *Oxycaryum cubense*, *Websteria confervoides*) or cosmopolitan (e.g. *Bolboschoenus maritimus*, *Cladium mariscus*) distribution.

The majority of Cyperaceae (265 species) occur in open habitats and are mostly C_4 taxa in the Cypereae and Abildgaardieae (table 1). A number of C_3 taxa inhabiting open habitats are hemicryptophytes, growing in wetlands, or therophytes growing in seasonally wet habitats. Therophytes comprise about 20% of the sedge flora in Madagascar, with a C_3/C_4 ratio of 1:2. *Carex* (twenty out of 33 species), *Costularia* (five out of eight), *Hypolytrum* (two out of two), *Schoenoxiphium* (two out of two) and *Trichoschoenus* (one out of one)

Table 1 – Summary of Cyperaceae diversity in Madagascar showing total species number and proportion (%) of species scored for endemism, C₄ photosynthesis, forest habitat and annual life form.

Tribe	Genus	Species	Endemics	C ₄	Forest	Annual
Cypereae	<i>Cyperus</i>	100	36	67	19	10
Cariceae	<i>Carex</i>	33	88	0	61	0
Sclerieae	<i>Scleria</i>	27	22	0	22	26
Cypereae	<i>Pycreus</i>	26	38	100	0	38
Abildgaardieae	<i>Bulbostylis</i>	21	71	100	0	62
Abildgaardieae	<i>Fimbristylis</i>	17	12	100	0	18
Cypereae	<i>Kyllinga</i>	13	8	100	0	8
Eleocharideae	<i>Eleocharis</i>	11	0	9	0	9
Fuireneae	<i>Schoenoplectiella</i>	10	50	0	0	50
Rhynchosporae	<i>Rhynchospora</i>	10	10	10	0	10
Fuireneae	<i>Fuirena</i>	8	25	0	0	13
Schoeneae	<i>Costularia</i>	8	100	0	63	0
Cypereae	<i>Lipocarpha</i>	5	0	100	0	80
Cypereae	<i>Isolepis</i>	4	25	0	0	25
Schoeneae	<i>Machaerina</i>	4	25	0	0	0
Fuireneae	<i>Schoenoplectus</i>	3	0	0	0	0
Cariceae	<i>Schoenoxiphium</i>	2	50	0	100	0
Cypereae	<i>Ascolepis</i>	2	0	100	0	50
Cypereae	<i>Courtoisina</i>	2	0	0	0	100
Hypolytreae	<i>Hypolytrum</i>	2	50	0	100	0
Abildgaardieae	<i>Actinoschoenus</i>	1	0	0	0	0
Abildgaardieae	<i>Trichoschoenus</i>	1	100	0	100	0
Bisboeckelereae	<i>Diplacrum</i>	1	0	0	0	100
Chrysitricheae	<i>Lepironia</i>	1	0	0	0	0
Cladieae	<i>Cladium</i>	1	0	0	0	0
Cypereae	<i>Alimula</i>	1	0	100	0	100
Cypereae	<i>Ficinia</i>	1	100	0	0	0
Cypereae	<i>Oxycaryum</i>	1	0	0	0	0
Cypereae	<i>Queenslandiella</i>	1	0	100	0	100
Cypereae	<i>Remirea</i>	1	0	100	0	0
Eleocharideae	<i>Websteria</i>	1	0	0	0	0
Fuireneae	<i>Bolboschoenus</i>	1	0	0	0	0
Trilepideae	<i>Coleochloa</i>	1	0	0	0	0

are predominantly found in forest habitats. Other genera well represented in forest habitats are *Cyperus* (nineteen out of 98) and *Scleria* (six out of 27 species). All forest Cyperaceae are hemicryptophytes with C₃ photosynthesis.

There are 121 endemic species (37% of the sedge flora), the largest number belonging to *Cyperus* (36% of the species in the genus in Madagascar) and *Carex* (88% of the species in the genus in Madagascar). *Costularia*, a genus also occurring in South Africa and New Caledonia, is notable in having all the eight Madagascan species being endemic. About 35% of the endemics are hemicryptophytes that occur in forests, belonging to *Carex* (seventeen species), *Cyperus* (fifteen species), *Costularia* (five species), and *Scleria* (three species). Of the remaining (non-forest) endemic species, 29% are C₃ hemicryptophytes in open habitats, whereas 36% are

C₄ therophytes (fifteen species) or hemicryptophytes (28 species). The C₄ taxa are mostly members of the tribe Cypereae (26 species) and Abildgaardieae (seventeen species).

Among the non-endemic species, Madagascar shares most species with tropical eastern Africa (Tanzania 142 species, Kenya 109 and Uganda 101), as well as tropical West Africa (Nigeria 102 species, Senegal 87), West Central Africa (D.R.Congo 97 species), Southern Africa (KwaZulu-Natal 86 species) and the Indian subcontinent (India 88 species) (fig. 1). Comparison of species shared between Madagascar and other countries – increasing from a single country to 5% of the TDWG countries – shows shared species with adjacent countries in African continent (fig. 2A), increasingly including more countries in sub-Saharan Africa, India and Australia (fig. 2B & C), to pantropical (fig. 2D) distribution pattern.

DISCUSSION

Madagascar is renowned for high species richness and unparalleled levels of endemism. Among the angiosperms, total species richness among the top ten largest families appears to be proportional to global species richness in these families. The total number of Cyperaceae species (321 out of 5,400 species) places the family as the 10th largest in Madagascar, and is comparable in species richness to Melastomataceae, on Madagascar and worldwide (321 and ~ 5,000 species respectively; Almeda 2003). On the other hand, endemism in Cyperaceae (37%) is much lower than endemism in other large families, for example Melastomataceae (99%). The non-endemic Cyperaceae are mostly pantropical (figs 1 & 2) and the family is nearly absent in humid (lowland) forests, habitats that harbour the bulk of endemic species in Melastomataceae and other families with high endemism in Madagascar.

The sedge flora in Madagascar is most similar to tropical Africa and India. This similarity cannot be explained by distance – KwaZulu-Natal has as many shared species as India that is nine times further away. Similarity between the biota in Madagascar region and in Asia (including India), majority of which are too young to be explained by vicariance, has been hypothesized to be due to availability of stepping-stones (Islands in the Indian Ocean over time) and regional processes (wind and current directions) (Warren et al. 2010). In addition, several lineages appear to have dispersed to habitats similar to ancestral areas (niche conservatism; Wiens & Graham 2005), e.g. *Isolepis* and *Ficinia* occurring in alpine habitats similar to the Western Cape of South Africa.

Kenya, a country of comparable size, has 275 Cyperaceae species (World Checklist of Monocotyledons 2010) comprising similar tribes except for Hypolytreae and Schoeneae. The two floras differ in the number of taxa occurring in forest

habitats (9% in Kenya vs. 17% in Madagascar), annual life-form (26% vs. 20%) and C₄ photosynthesis (63% vs. 36%). Madagascar has seven times more endemic species than Kenya (37% vs. 6%), with a large number of forest habitat species whereas none of the endemics in Kenya occur in forests. Kenya has predominantly savannah endemics which are mostly C₄ hemicryptophytes in *Kyllinga* and *Cyperus*.

The species endemism of Cyperaceae in Madagascar is notable at the global level (electronic appendix 2). When TDWG level 3 countries are rescaled to eliminate the bias of area, Madagascar is second to Cape Provinces in highest number of endemic species (Muasya et al. unpubl.). Many of the endemic species occur in high altitude forest habitats – richest in *Carex* subgenus *Vigneastra* and C₃ *Cyperus* lineages – than the open (and mostly drier) habitats. The savannah grasslands of Madagascar are particularly species poor and lack endemics among the Cyperaceae, pointing to potential lack of speciation in this habitat. Whereas the antiquity of Madagascar C₄ grasslands and savannah has been demonstrated (e.g. Bond et al. 2008, Willis et al. 2008), it is puzzling that there is no comparable diversification of characteristic lineages (e.g. *Kyllinga*; electronic appendix 3) in this habitat when compared to tropical Africa. This points either to a recent origin of savannah grasslands or to anthropogenic disturbances which may obscure diversity patterns. Widespread conversion of wetlands into paddy fields may lead to extinction of species with narrow ranges and favours widespread taxa thriving in eutrophic conditions.

Part of the sedge endemism in open habitats can be explained by the large geological diversity of Madagascan landscapes. The largest proportion of open wetland endemics belongs to C₄ genera *Bulbostylis* and *Pycneus*. When compared to related C₄ lineages, *Bulbostylis* and *Pycneus* are known to be capable of adapting to habitats with high chemical stress

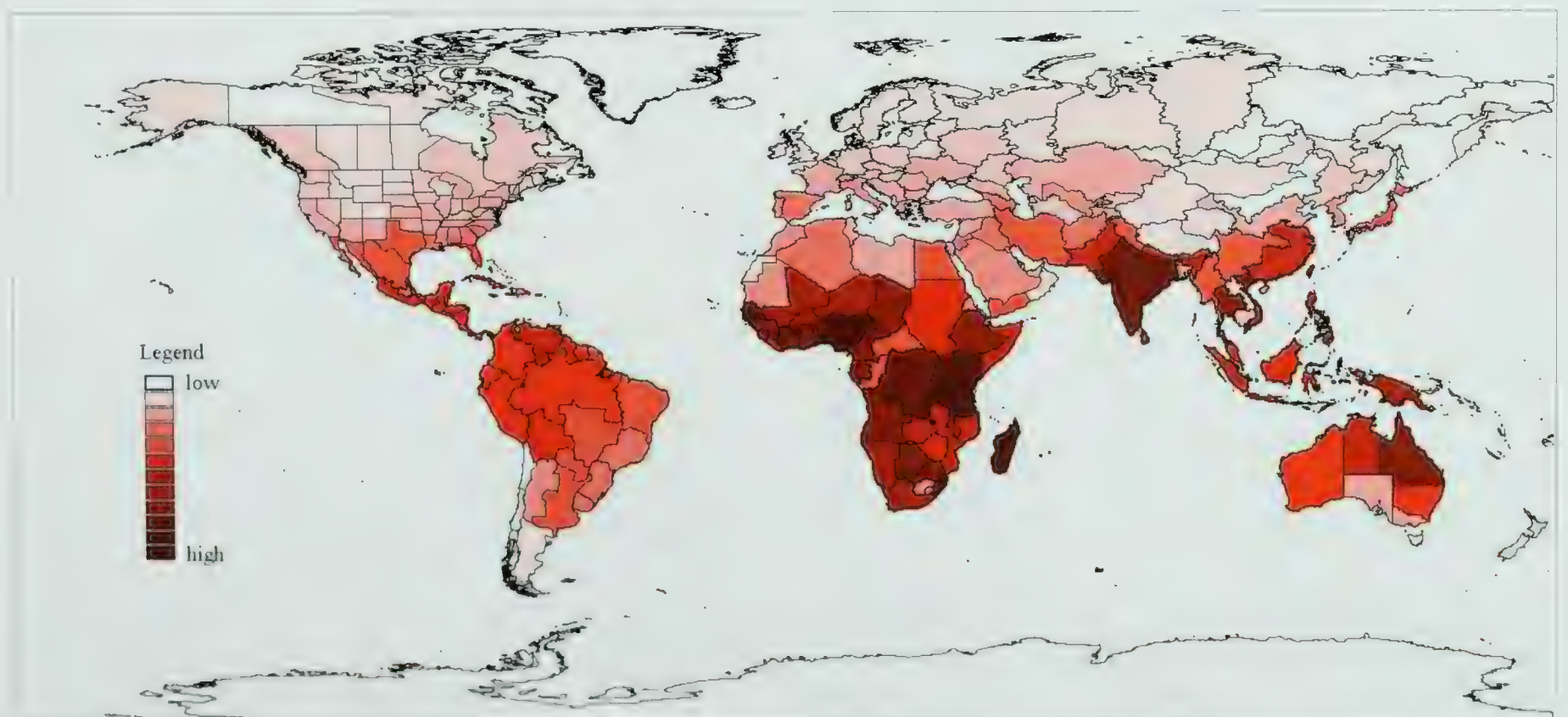


Figure 1 Cyperaceae species shared by Madagascar and other TDWG level 3 countries using the 314 species recorded in the World Checklist of Monocotyledons (2010). The seven additional taxa, recently recorded, were not plotted (electronic appendix 1). Colour coding range from white (0 species) to dark red (314 species).

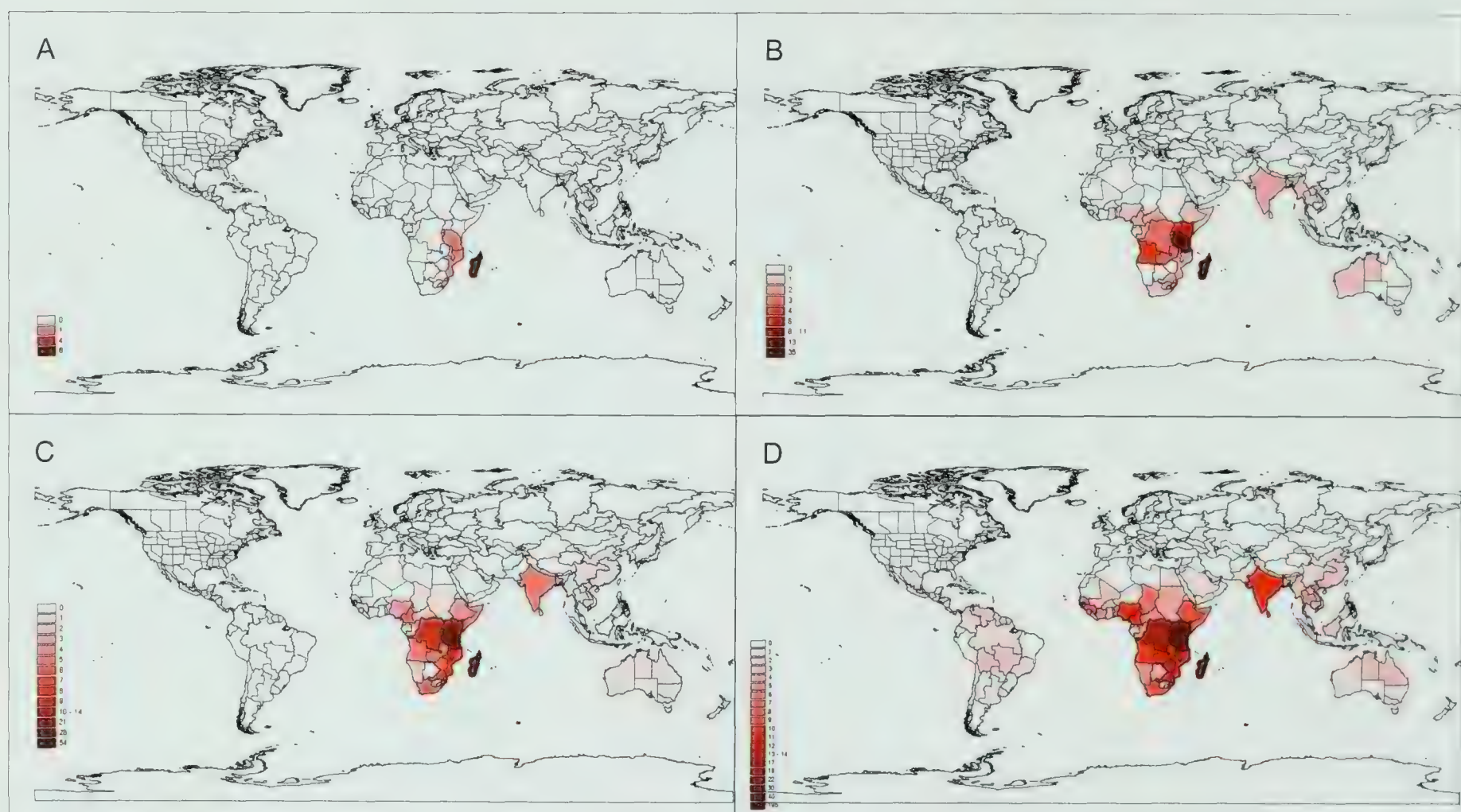


Figure 2 – Comparisons of species occurrence: A, species distributed in Madagascar and 3 other TDWG botanical countries (= 1% of all countries); B, in Madagascar and 5% of all countries; C, in Madagascar and 10% of all countries; D, in Madagascar and 25% of all countries.

(including salinity, heavy metals, acidity; e.g. Leteinturier et al. 1999). In Madagascar, *Pycnus* has three endemics on coastal sand dunes, two on limestone and one on volcanic hot springs and several species in bogs. *Bulbostylis* is also highly diversified on drier, rocky and sandy habitats (Chermezon 1937).

The forest habitats of Madagascar are occupied mainly by lineages that have stem node ages in the Neogene (Besnard et al. 2009, Muasya et al. unpubl.) whereas older forest lineages are absent (*Mapania*) or poorly represented (*Hypolytrum*). Members of *Cyperus* sect. *Incurvi* (Larridon et al. 2011), show several convergent morphologies, and fill the niches which are occupied elsewhere by Mapanioids. This implies that the assembly of the sedge flora in Madagascar has occurred recently, involving the dispersal into and subsequent diversification within the forest habitat. It might also indicate that the formation of the wet forest biome has only occurred in the Tertiary. This is also supported by the view of Wells (2003) that evergreen and deciduous forests, montane types and grasslands have evolved subsequent to the positioning of Madagascar in the tropics.

Biodiversity studies of Madagascar have focussed on charismatic plant families, perhaps skewing the view of species richness and endemism in less conspicuous lineages such as the Cyperaceae. As the family is mostly under-collected and is taxonomically poorly known, the full picture on diversity patterns may change as more focused studies become available. Endemism in open wetland or afro-alpine lineages of *Bulbostylis* and *Pycnus* may be overestimated for Madagascar, with several endemic species likely to be conspecific with taxa in poorly studied areas in mainland Africa

(D.R.Congo, Mozambique). However, the evidence for a young wet forest and highland sedge flora is an interesting pattern that is worth investigating in greater detail.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consist of the following: (1) Full species list for Cyperaceae in Madagascar (pdf); (2) Cyperaceae endemics in to Top 20 TDWG-level 3 botanical countries (pdf); and (3) Comparison of *Kyllinga* species richness in Madagascar and Kenya (pdf).

ACKNOWLEDGEMENTS

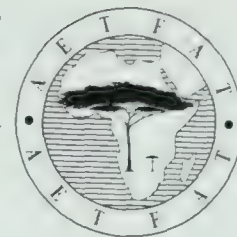
Field observations were facilitated by research permit (Isabel Larridon: N°082/10/MEF/SG/DGF/DCB.SAP/SLRSE). The field expedition was financed (IL, MR, WH) through travel grants of the Research Foundation - Flanders (FWO) and support of the Department of Biology, Ghent University, Belgium. AMM received financial support from the South African National Research Fund (incentive funding). We acknowledge logistical support from the ANGAP Madagascar National Parks authority, and the general secretariat of the AETFAT Congress 2010 and the staff of the MBG office in Antananarivo for their help in securing collecting permits for Cyperaceae in Madagascar and their help organising the expedition.

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Manuscript received 31 Oct. 2010; accepted in revised version 22 Aug. 2011. This paper was pre-published on 15 Nov. 2011 in issue 144(3) of *Plant Ecology and Evolution*.

Communicating Editor: Steven Dessein.



Analyse phytogéographique des forêts d'Afrique Centrale: le cas du massif de Ngovayang (Cameroun)

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Phytogeographical analysis of Central African forests: the Ngovayang massif (Cameroon)

Background and aims – The Ngovayang massif, in southern Cameroon, is part of a group of small hills along the Atlantic coast of the Gulf of Guinea. This area is known for its floristic richness and its high level of endemism. We conducted a phytogeographical analysis of this massif and evaluated its floristic affinities with other forested sites in Central Africa.

Methods – Phytogeographical analysis was based on a comparison of lists of tree species with dbh $\geq$ 10 cm, inventoried in 1-ha permanent plots, and established in old growth lowland forests of Central Africa. The floristic list for Ngovayang used for this analysis contained 201 species.

Key results – The lowland forests of the Ngovayang massif are dominated by Leguminosae-Caesalpinioideae, followed by Olacaceae and Burseraceae, taxa characteristic of dense old-growth Atlantic moist forests. The Ngovayang flora includes a high proportion of Guineo-Congolese species (79%), particularly Lower Guinean species (30%). Phytogeographical analysis showed that forested sites of central Africa are clearly separated into continental sites and the more coastal sites of the Lower Guinean domain, including Ngovayang. Within the Lower Guinean domain, the main floristic discontinuity appears to be situated in southern Cameroon-northern Equatorial Guinea. Ngovayang and Takamanda, which are situated on opposite sides of the Cameroon volcanic line, show stronger floristic affinities with each other than either does with other Lower Guinean forest sites located to the south of the Ngovayang massif.

Conclusions – Ngovayang may constitute a transition zone between Nigerian forests and those ranging from southern Cameroon to the Democratic Republic of the Congo. For tree species of the Lower Guinean domain, the climatic hinge separating boreal and austral climates appears to be a more important phytogeographic barrier than the Cameroon volcanic line or the Sanaga River.

Key words – Central Africa, Ngovayang, phytogeography, climatic hinge, 1-ha permanent plots.

Objectifs – Le massif de Ngovayang (Sud-Cameroun) fait partie des petits sommets qui longent le golfe de Guinée. Cette région est connue pour sa forte richesse floristique et son taux d'endémisme élevé. Ce travail a pour objectif une analyse phytogéographique de ce massif et l'évaluation de ses affinités floristiques avec d'autres sites forestiers d'Afrique centrale atlantique.

Méthodes – L'analyse phytogéographique fut basée sur la comparaison des listes d'espèces d'arbres de dbh $\geq$ 10 cm, issues de parcelles permanentes de 1-ha établies dans des forêts matures de basse et moyenne altitude d'Afrique centrale atlantique. La liste floristique du massif de Ngovayang retenue pour cette analyse comprend 201 espèces d'arbres.

Résultats-clés – Les forêts de basse altitude du massif de Ngovayang sont dominées par les Leguminosae-Caesalpinioideae, suivies des Olacaceae et des Burseraceae, tous taxons caractéristiques des forêts matures denses humides atlantiques. La flore de Ngovayang compte une forte proportion d'espèces

guinéo-congolaises (79%) et plus particulièrement d'espèces guinéennes inférieures (30%). L'analyse phytogéographique montre qu'il existe dans la région étudiée une séparation nette entre les sites continentaux et les sites côtiers du domaine bas-guinéen, y compris le massif de Ngovayang. A l'intérieur du domaine bas-guinéen, la discontinuité floristique la plus importante apparaît aux confins du Sud-Cameroun et du Nord de la Guinée-Equatoriale. Ngovayang et Takamanda, situés de part et d'autre de la ligne volcanique du Cameroun, présentent de plus fortes affinités floristiques entre eux qu'avec les autres forêts situées au sud du massif de Ngovayang.

Conclusion – Ngovayang pourrait constituer une zone de transition importante entre les forêts du Nigéria et celles s'étendant du Sud-Cameroun jusqu'en République Démocratique du Congo. La charnière climatique séparant les climats boréal et austral semble constituer une barrière phytogéographique plus importante pour les arbres des forêts de basse altitude que la ligne volcanique du Cameroun ou le fleuve Sanaga.

INTRODUCTION

Les forêts tropicales humides africaines font partie des écosystèmes les plus importants, les plus complexes et les plus riches de la planète (Wilson 1995, van Gemerden 2004). La région guinéo-congolaise, qui couvre une superficie de 2,8 millions de km², s'étend du sud du Sénégal à l'ouest de l'Ouganda et au nord de l'Angola, et renferme le principal massif de forêts denses humides d'Afrique, avec plus de 80% de plantes endémiques (White 1983). Ces forêts présentent une grande gamme de variation, tant en termes de phénologie (forêts sempervirentes à semi-décidues) que de composition floristique. Au sein de cet ensemble, les deux plus importantes subdivisions floristiques correspondent, d'une part, aux forêts situées à l'intérieur et en périphérie de la cuvette congolaise – les forêts 'congolaises' – et, d'autre part, à celles situées en Afrique occidentale et en Afrique centrale atlantique, les forêts 'guinéennes'.

Ces forêts guinéennes sont séparées en deux blocs par l'avancée des savanes jusqu'à la côte atlantique, au Togo et au Bénin: un domaine floristique 'haut-guinéen' ou guinéen supérieur (Afrique occidentale) et un domaine 'bas-guinéen' ou guinéen inférieur (Afrique centrale autour du Golfe de Guinée; White 1979). Les forêts sempervirentes côtières, le long du littoral atlantique africain, de la Sierra Leone jusqu'à l'ouest du Gabon, bénéficient des climats les plus humides, avec des précipitations annuelles qui peuvent dépasser 2000 mm. Ces forêts renferment une flore très riche avec un taux d'endémisme élevé (Aubréville 1958, 1962, Hall & Swaine 1976, 1981, White 1983, Letouzey 1985, Hawthorne 1995, Doumenge et al. 2003).

Le domaine bas-guinéen a été à son tour subdivisé en deux secteurs phytogéographiques: le secteur du bassin sédimentaire côtier (forêts littorales) et celui des collines atlantiques (forêts biafréennes de Letouzey 1968, 1985, Caballé 1978, Doumenge et al. 2001). Ces collines atlantiques forment un archipel qui borde, en retrait, le littoral atlantique depuis le Cameroun jusqu'en République Démocratique du Congo (RDC). Les principaux sommets n'y dépassent guère 1000 m d'altitude, et incluent: les monts Rumpi, le massif de Ngovayang et la région de Campo-Ma'an (Cameroun), la région du Monte Alén et du Monte Mitra (Guinée Equatoriale), les monts de Cristal et les monts Doudou (Gabon), le massif du Chaillu (Gabon et Congo) ainsi que la chaîne du Mayombe (du Gabon à la RDC; fig. 1).

Si les schémas biogéographiques développés par certains auteurs (Monod 1957, Lebrun 1960, 1961, White 1983) restent tout à fait d'actualité à l'échelle du continent, ils se montrent largement perfectibles à l'échelle de secteurs phytogéographiques plus restreints comme le bas-guinéen. Des études phytogéographiques plus fines ont été réalisées à l'échelle des pays, à l'instar de Letouzey (1968, 1985) pour le Cameroun, Caballé (1978) pour le Gabon, Senterre (2001) pour la Guinée équatoriale et Lubini (1997, 2001) pour la RDC. Certains de ces travaux sont basés sur la chorologie (répartition des espèces), d'autres sur des inventaires écologiques ou phytosociologiques. Les travaux de synthèse à l'échelle de la région guinéo-congolaise ou de ses subdivisions, basés sur des méthodes d'échantillonnage, quantifiées et comparables, font encore largement défaut. La seule tentative, récente, est celle de Senterre (2005), qui a comparé plusieurs forêts le long d'un méga-transect partant de l'océan atlantique jusque dans la Réserve de biosphère du Dja. Ce travail donne un premier aperçu quantifié de la variation du peuplement arboré de ces forêts, mais reste encore très insuffisant pour une comparaison exhaustive des affinités floristiques sur l'ensemble du secteur floristique guinéen, voire bas-guinéen.

Par ailleurs, des études biogéographiques ou des révisions taxonomiques limitées à certains groupes systématiques, encore trop peu nombreuses, apportent aussi un éclairage complémentaire dans l'analyse des affinités floristiques entre les forêts de cette région. Il s'agit des travaux sur certaines familles telles que les Euphorbiaceae (Léonard 1965) et les Orchidaceae du domaine bas-guinéen (Droissart 2009), la révision des genres *Annickia* (Annonaceae; Versteegh & Sosef 2007), *Anthonothea* (Leguminosae-Caesalpinioideae; Breteler 2010), *Baphia* (Leguminosae-Faboideae; Soladoye 1985), *Begonia* (Begoniaceae; Sosef 1994) ou *Diospyros* (Ebenaceae; White 1978). Il ressort néanmoins de ces travaux que tous les petits reliefs bordant la côte atlantique possèdent en commun une caractéristique: l'abondance de Leguminosae-Caesalpinioideae grégaires (White 1983, Letouzey 1985, Senterre 2001, 2005). S'il est établi qu'il existe des différences entre les forêts continentales du domaine congolais et celles, plus côtières, du domaine guinéen (Letouzey 1968, White 1983, Senterre 2005), la variation floristique et les affinités phytogéographiques fines, depuis les forêts bordant la ligne volcanique du Cameroun (LVC) jusqu'au Mayombe congolais demeurent mal connues. La LVC, constituée de grands sommets montagneux (Mont Cameroun, Mont Oku,

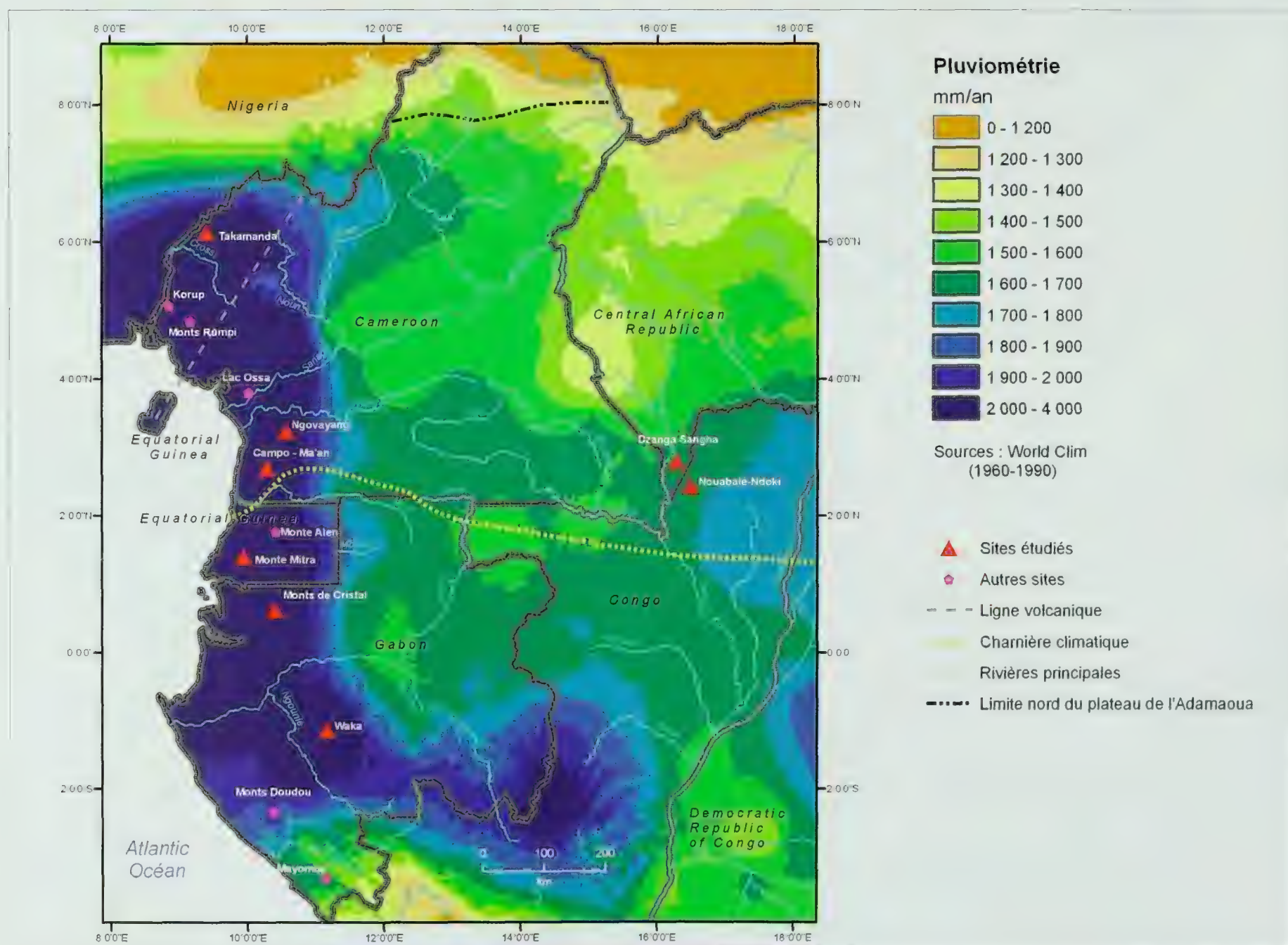


Figure 1 – Localisation du massif de Ngovayang et des autres sites étudiés en Afrique Centrale. Charnière climatique adaptée d'après Suchel (1990). Carte réalisée par le Cirad en Janvier 2012.

Mont Kupé...), et le fleuve Sanaga ont-ils pu jouer le rôle de barrière entre les forêts des confins nigéro-camerounais et celles situées à l'Est de la LVC et plus au Sud? Le basculement climatique qui se produit à l'extrême Sud du Cameroun, entre climat d'hémisphère Nord et climat d'hémisphère Sud, matérialisé par la 'charnière climatique' (Saint-Vil 1984, Suchel 1990, Fontaine & Bigot 1993, Wotling et al. 1995, Bigot et al. 1997, Thomas & Goudie 2000, Balas et al. 2007), influence-t-il la composition floristique de ces forêts?

Le massif forestier de Ngovayang (alt. 50–1090 m), situé à la charnière entre la LVC et l'ensemble des collines descendant du Sud-Cameroun jusqu'en RDC, est idéalement situé pour tenter de répondre à ces questions et nous permettra d'explorer les relations phytogéographiques entre les forêts de tout cet ensemble floristique bas-guinéen. Par ailleurs, ce massif, bien qu'il ait fait l'objet d'une étude phytogéographique préliminaire (Letouzey 1985), demeure toujours peu exploré. Les premiers travaux d'inventaires botaniques, très localisés, concernaient uniquement des collectes botaniques (en particulier celles de Zenker, entre 1896 et 1922). D'autres études, plus récentes, ont porté sur les collections de spécimens botaniques nécessaires à l'étude de certains groupes taxonomiques, notamment les Orchidaceae

(Droissart 2009) et les Rubiaceae (Sonké et al. 2006a, 2006b, 2008). Aucun inventaire quantifié de la végétation n'avait été réalisé avant la présente étude.

Sur la base d'inventaires quantifiés des peuplements arborés, nous nous proposons donc d'analyser la position phytogéographique du massif de Ngovayang et de préciser ses affinités floristiques avec d'autres massifs forestiers d'Afrique Centrale, en particulier dans le secteur floristique de Basse-Guinée.

MÉTHODES

Site d'étude

Le massif montagneux de Ngovayang se situe dans le Sud du Cameroun, à environ 80 km de la côte atlantique. Il s'étend sur 102 000 ha, entre les parallèles 3°12'–3°25'N et les méridiens 10°30'–10°45'E (fig. 1). L'altitude varie entre 50 m, dans la partie sud-ouest, et 1090 m dans la partie centre-est, sur les plus hauts sommets. La géomorphologie du massif est très complexe, constituée d'un ensemble de crêtes dis-séquées d'orientation principale sud-ouest/nord-est. Le versant sud-est est caractérisé par des pentes abruptes tandis que des piedmonts d'altitudes variées occupent le versant

nord-ouest. Le socle précambrien constitue le soubassement géologique du massif, caractérisé par des roches métamorphiques acides (gneiss, migmatites, quartzites et schistes) traversées par des intrusions de roches basiques et de vieilles roches volcaniques tels que les diorites et les gabbros (Franqueville 1973).

Le climat est de type sub-équatorial (Suchel 1972). Les précipitations moyennes annuelles sont de l'ordre de 2000 mm (Waterloo et al. 2000). Elles diminuent avec l'augmentation de la distance par rapport à l'océan de 2836 mm $\pm$ 393 à Kribi, situé environ 80 km à l'ouest de l'extrémité sud-ouest du massif de Ngovayang, à 2150 mm $\pm$ 286 à Eséka (environ 15 km au nord de l'extrémité nord-est du massif; Olivry 1986). Deux minima et maxima pluviométriques annuels distincts sont observés et sont associés avec les mouvements nord-sud de la zone de convergence intertropicale (ZCIT): une petite saison sèche (mi-mai à mi-août) et une grande saison sèche (mi-novembre à mi-mars) qui séparent les deux saisons des pluies (mi-mars à mi-mai pour la petite saison des pluies et mi-août à mi-novembre pour la grande saison des pluies). La température moyenne annuelle est de 25°C (Waterloo et al. 2000). Le réseau hydrographique, très dense, est constitué de nombreuses petites rivières entrecoupées de chutes.

Les forêts atlantiques biafréennes riches en Leguminosae-Caesalpinioideae constituent le principal type de formation végétale rencontré dans la zone d'étude (Letouzey 1968, 1985). En sus des menaces globales tels que les changements climatiques, la destruction de la forêt pour des besoins en terres cultivables et l'exploitation du bois ont contribué à la destruction de la végétation naturelle depuis des décennies, principalement dans les zones basses et plates facilement accessibles (Letouzey 1985). Des forêts secondaires se sont fréquemment développées dans ces régions de basse altitude, en dessous de 300 m. D'autres pressions humaines, telles que la chasse ou la cueillette de produits forestiers, sont aussi notables, y compris en altitude. Cependant, en raison de sa topographie accidentée et de sa faible densité démographique, le massif de Ngovayang a été jusqu'ici relativement préservé de ces menaces et de vastes étendues de forêts très peu ou non perturbées y subsistent encore.

Collecte des données

L'analyse floristique et phytogéographique a été basée sur l'inventaire du peuplement arboré de parcelles permanentes de 1 ha (100 m $\times$ 100 m). Ces parcelles ont été installées dans plusieurs sites d'Afrique Centrale, à savoir: la réserve forestière de Takamanda (6 parcelles) et le massif de Ngovayang (5 parcelles) au Cameroun, le Monte Mitra (3 parcelles) en Guinée Equatoriale, les monts de Cristal (5 parcelles) et le parc national de Waka (2 parcelles) au Gabon, le parc national de Nouabalé-Ndoki (3 parcelles) au Congo et le parc national de Dzanga-Sangha (une parcelle) en République Centrafricaine (fig. 1).

Dans ces parcelles, tous les arbres dont le diamètre du tronc à hauteur de poitrine (dhp, mesuré à 1,3 m du sol pour les arbres sans contreforts et sans anomalies) était supérieur ou égal à 10 cm ont été identifiés et mesurés. Le protocole et les détails de mesure suivent les recommandations en

vigueur (Dallmeier et al. 1992, White & Edwards 2001). De plus en plus utilisé en Afrique Centrale, ce protocole facilite les comparaisons entre les sites. Dans le massif de Ngovayang, les spécimens d'herbier ont été récoltés pour la plupart des espèces recensées en vue de confirmer les identifications de terrain. Les identifications botaniques ont été réalisées à l'aide des flores existantes et les échantillons ont été comparés aux spécimens de référence de l'Herbier National du Cameroun. Afin d'homogénéiser les données, les listes d'espèces utilisées pour les analyses comparatives des sites étudiés sont issues uniquement des parcelles installées dans les forêts les plus matures possibles, sur terre ferme et d'altitude inférieure à 700 m. Les forêts ayant subies un impact humain (forêts secondaires, forêts exploitées) et celles dépendantes de conditions environnementales particulières (forêts inondables et forêts d'altitude) ont été exclues de l'étude pour faciliter les comparaisons entre les différents sites.

Analyse floristique

Deux indices d'importance écologique des espèces et des familles ont été calculés pour les parcelles du massif de Ngovayang, pour lesquelles nous disposons des données d'abondance: l'*Importance Value Index* (IVI; Curtis & McIntosh 1951) et le *Family Importance Value Index* (FIV; Mori et al. 1983). Des détails sont donnés en matériel supplémentaire (appendice électronique 3).

Analyse phytogéographique

Les données relatives aux aires de répartition des espèces sont issues de la bibliographie, à savoir, les flores (Keay & Hepper 1954–1972, Aubréville & Leroy 1961–1992, 1963–1978, Hallé 1961–1987, Letouzey 1968, 1985, Lebrun & Stork 1991–1997) et d'autres publications (White 1983, Sonké 2005, Senterre 2005, Tchouto 2004), ainsi que les bases de données en ligne (Conservatoire du Jardin Botanique de Genève: <http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php>).

L'analyse phytogéographique a porté sur 201 taxons déterminés au niveau de l'espèce. Les différents types d'aires de répartition retenus sont basés sur la classification de White (1979, 1983).

A. Espèces à large distribution

Cosmopolites: espèces réparties dans le monde entier, aussi bien dans les zones tempérées que tropicales;

Pantropicales: espèces présentes en Afrique, Amérique et Asie tropicales;

Afro-américaines: espèces répandues en Afrique et Amérique tropicales;

Paléotropicales: espèces connues en Afrique et Asie tropicales ainsi qu'à Madagascar et en Australie;

Afromalgaches: espèces communes aux îles de la région malgache et de l'Afrique continentale.

B. Espèces de liaison

Espèces dont l'aire de distribution couvre deux ou plusieurs régions floristiques africaines et qui sont trop largement répandues ou trop abondantes par endroits pour être considérées comme des sub-endémiques. Ces éléments

sont soit des transgresseurs chorologiques et écologiques, soit simplement des espèces à large distribution et à écologie assez uniforme.

C. Espèces sub-endémiques guinéo-congolaises
Espèces qui s’étendent aux zones de transitions adjacentes ou qui débordent légèrement au-delà de ces dernières en tant qu’espèces d’intrusion marginale ou en tant qu’espèces formant des peuplements satellites faiblement éloignés.

D. Espèces endémiques guinéo-congolaises
Omni-guinéo-congolaises: présentes dans toute la région guinéo-congolaise;
Omni-guinéennes: présentes dans les domaines guinéens inférieur et supérieur;
Centro-guinéo-congolaises: espèces dont la distribution couvre les domaines guinéen inférieur (du sud du Nigeria à la République Démocratique du Congo) et congolais;
Guinéennes inférieures: espèces répandues dans le sous-centre guinéen inférieur, du sud du Nigeria au sud de la République du Congo;
Endémiques camerounaises: espèces exclusivement camerounaises.

La nomenclature botanique utilisée est celle adoptée par Lebrun & Stork (1991–1997), afin de pouvoir comparer les résultats avec la bibliographie, en particulier lorsqu’il s’agit de certaines familles importantes (Olacaceae et Euphorbiaceae) qui ont été éclatées dans le système de classification d’APGIII, ou d’autres qui ont été mises ensemble (Bombacaceae, Sterculiaceae et autres, dans la famille Malvaceae *sensus* APGIII). Les autorités taxonomiques de toutes les espèces nommées dans cette étude sont données en matériel supplémentaire (appendices électroniques 1 & 2).

La classification des relevés a été réalisée en fonction de l’indice de dissimilarité de Bray-Curtis binaire (BC_{ij}) en utilisant la bibliothèque Vegan du logiciel R 2.10.1 (Oksanen et al. 2010); des détails sont donnés en matériel supplémentaire (appendice électronique 3).

Cette première analyse nous a permis d’identifier des groupes de relevés proches sur la base d’occurrence d’espèces (données de présence / absence), à partir des listes d’espèces inventoriées dans chaque site. La distance entre les relevés varie de 0 (relevés identiques, compositions floristiques identiques) à 1 (relevés sans recouvrement, compositions floristiques complètement différentes, aucune espèce commune).

Une classification ascendante hiérarchique sur la base des méthodes agglomératives à liens complets, a été utilisée pour la construction du dendrogramme de ressemblances entre les relevés.

RESULTATS

Richesse et composition floristique globale des forêts de Ngovayang

Les cinq parcelles installées dans les forêts de basse altitude du massif forestier de Ngovayang ont permis de recenser au total 2658 individus à dhp $\geq$ 10 cm correspondant à 293 espèces et morpho-espèces, 170 genres et soixante familles.

Tableau 1 – Spectre phytogéographique des espèces du massif de Ngovayang.

Les grands groupes phytogéographiques sont précédés des lettres A, B, C et D. Ils sont classés du type le plus large au plus restreint.

Type phytogéographique	Nombre d'espèces	Proportion (%)
A. Espèces à large distribution	4	2
Cosmopolites	0	0
Pantropicales	0	0
Paléotropicales	0	0
Afro-américaines	2	1
Afro malgaches	2	1
B. Espèces de liaison	20	10
C. Espèces sub-endémiques guinéo-congolaises	18	9
D. Espèces guinéo-congolaises	159	79
Omni-guinéo-congolaises	34	17
Centro-guinéo-congolaises	45	22
Omni-guinéennes	17	8
Guinéennes inférieures	60	30
Endémiques camerounaises	3	2
Nombre total d'espèces	201	100

Parmi ces 293 espèces, 201 ont été déterminées au niveau spécifique, 82 au niveau du genre et dix espèces restent indéterminées.

Les familles les plus riches en espèces sur la base des 293 taxons sont les Euphorbiaceae (36 espèces, soit 12% de la flore), la sous-famille des Leguminosae-Caesalpinioideae (23 espèces, soit 8% de la flore) et les familles des Ebenaceae (19 espèces), des Annonaceae (quatorze espèces), des Rubiaceae (treize espèces), des Olacaceae (onze espèces) et des Clusiaceae (dix espèces). Les Leguminosae-Caesalpinioideae représentent la (sous-)famille la plus importante en termes de FIV. Elle est suivie de près et en valeur décroissante par la famille des Euphorbiaceae, des Clusiaceae, des Myristicaceae, des Olacaceae, des Ebenaceae, des Annonaceae et des Burseraceae. On note aussi la présence des Leguminosae-Caesalpinioideae grégaires, représentées surtout par *Didelotia letouzeyi*, *Guibourtia tessmannii* et *Tetraberlinia bifoliolata* (Gonmadje et al. 2011).

Spectres phytogéographiques des forêts de Ngovayang

L’analyse phytogéographique des forêts de basse et moyenne altitude du massif de Ngovayang montre que les espèces guinéo-congolaises sont largement majoritaires dans le fond floristique de la zone d’étude avec 79% des espèces (tableau 1). A part un très petit pourcentage d’espèces à large répartition (2%), les 19% restants sont soit des espèces sub-endémiques au centre d’endémisme guinéo-congolais, soit des espèces de liaison avec les régions phytogéographiques adjacentes. Au sein de ces espèces guinéo-congolaises, les deux principaux groupes renferment, soit des espèces endémiques du domaine guinéen inférieur, soit des espèces

centro-guinéo-congolaises. Ces deux groupes constituent à eux seuls environ 52% de la flore.

Les espèces du domaine guinéen inférieur, caractéristiques des forêts entourant le golfe de Guinée, représentent 30% de la flore de Ngovayang. Parmi les espèces les plus importantes en termes d'IVI, on peut citer *Tetraberlinia bifoliolata* (Leguminosae-Caesalpinioideae), *Treculia obovata* (Moraceae), *Garcinia lucida* (Clusiaceae), *Didelotia letouzeyi* (Leguminosae-Caesalpinioideae), *Oubanguia alata* (Scytopetalaceae), *Cola rostrata* (Sterculiaceae), *Sibangea similis* (Euphorbiaceae), *Heisteria zimmereri* (Olacaceae) et *Garcinia mannii* (Clusiaceae). Dans ce groupe, une espèce endémique camerounaise a été collectée: *Tetraberlinia korupensis* (Leguminosae-Caesalpinioideae). Avant la présente étude, cette dernière espèce n'était connue que du parc national de Korup. Les familles les plus représentées sont les Euphorbiaceae (10% des espèces de Basse-Guinée présentes sur le site), les Sterculiaceae (7%), les Annonaceae (6%) les Rubiaceae (5%) et les Leguminosae, essentiellement la sous-famille des Caesalpinioideae (9%).

Les espèces centro-guinéo-congolaises représentent 22% de la flore et sont surtout représentées par *Drypetes gossweileri*, *Mareyopsis longifolia*, *Uapaca staudtii*, *Dichostemma glaucescens* (Euphorbiaceae), *Diospyros crassiflora*, *D. iturensis* (Ebenaceae), *Aidia micrantha*, *Aulacocalyx jasmiflora* (Rubiaceae), *Pentadesma grandifolia*, *Allanblackia floribunda* (Clusiaceae), *Aphanocalyx cynometroides*, *Gilbertiodendron ogoouense* (Leguminosae-Caesalpinioideae), et *Coelocaryon preussi* (Myristicaceae). Les Euphorbiaceae (27% des espèces), les Ebenaceae (9%), les Rubiaceae (9%) les Clusiaceae (6%) et les Leguminosae-Caesalpinioideae (6%) sont les mieux représentées.

Les espèces omni-guinéo-congolaises représentent 17% de la flore avec des espèces telles que *Mareya micrantha* (Euphorbiaceae), *Strombosia grandifolia* (Olacaceae), *Anthonotha fragrans* (Leguminosae-Caesalpinioideae), *Oncoba glauca* (Flacourtiaceae) et *Cola lateritia* (Sterculiaceae). Les familles des Olacaceae (12% des espèces), des Euphorbiaceae (9%), des Flacourtiaceae (9%), des Sterculiaceae (9%) et la sous-famille des Leguminosae-Caesalpinioideae (9%) sont les plus représentées dans ce type phytogéographique.

Environ 9% des espèces sont subendémiques guinéo-congolaises. Parmi elles, on peut citer: *Diospyros gabunensis* (Ebenaceae), *Hymenostegia afzelii* (Leguminosae-Caesalpinioideae), *Trichilia prieureana* (Meliaceae), *Discoglyprena caloneura* (Euphorbiaceae) et *Xylopia aethiopica* (Annonaceae).

Affinités floristiques avec divers autres sites d'Afrique centrale

La classification des espèces des différents sites étudiés permet de distinguer deux groupes principaux au seuil de dissimilarité de 96% (fig. 2):

- (1) un groupe formé par les deux sites continentaux: Dzanga-Sangha et Nouabalé-Ndoki,
- (2) un groupe formé par les cinq sites côtiers, du domaine guinéen inférieur. Dans ce groupe, on peut distinguer, à partir de 76% de dissimilarité, deux sous-groupes. Le

premier est constitué des sites situés au sud du massif de Ngovayang (monts de Cristal, Waka et Monte Mitra) et le second est formé par Ngovayang et Takamanda.

Parmi les taxa qui permettent de différencier les deux groupes sus-cités, les Leguminosae-Caesalpinioideae sont les plus représentés: *Berlinia craibiana*, *Didelotia letouzeyi*, *Guibourtia tessmannii*, *Leonardoxa africana* et *Tetraberlinia bifoliolata* sont uniquement présents dans les sites du domaine guinéen inférieur. D'autres espèces sont également typiques des forêts de Basse-Guinée, telles que *Poga oleosa* (Anisophylleaceae), *Calpocalyx dinklagei* (Leguminosae-Mimosoideae) et *Dacryodes buettneri* (Burseraceae).

Parmi les espèces du domaine guinéen inférieur recensées dans les divers sites, *Allophylus bullatus* (Sapindaceae), *Cleistanthus letouzeyi*, *Drypetes molunduana* et *Sibangea similis*, (Euphorbiaceae), *Cola anomala*, *C. megalophylla* et *C. semecarpophylla* (Sterculiaceae), et *Tetraberlinia korupensis* (Leguminosae-Caesalpinioideae) sont communes au massif de Ngovayang et à Takamanda mais elles n'atteignent pas les sites plus au Sud (monts de Cristal, Monte Mitra et Waka). Deux sous-espèces de *Leonardoxa africana* (Leguminosae-Caesalpinioideae) sont également présentes dans les sites du Nord: *Leonardoxa africana* subsp. *gracilicaulis* à Ngovayang et *Leonardoxa africana* subsp. *letouzeyi* à Takamanda. Seule, cette dernière est restreinte aux confins camerouno-nigériens, la sous-espèce *gracilicaulis* s'étendant au Sud vers la Guinée-Equatoriale et le Gabon (McKey 2000, Brouat et al. 2004). Par ailleurs, d'autres espèces ne sont présentes que dans les sites les plus au Sud; elles n'atteignent pas Ngovayang ni Takamanda. Il s'agit, par exemple, de *Bikinia durandii*, *Daniellia soyauxii*, *Hymenostegia pellegrinii*, et *Julbernardia brieyi* (Leguminosae-Caesalpinioideae), *Engomegoma gordonii* et *Strombosia sereinii* (Olacaceae), et *Aucoumea klaineana* (Burseraceae).

Lorsque l'on réalise le même type de comparaison au niveau des familles, la classification des relevés permet également de distinguer, à partir de 44% de dissimilarité, les deux mêmes groupes principaux observés précédemment

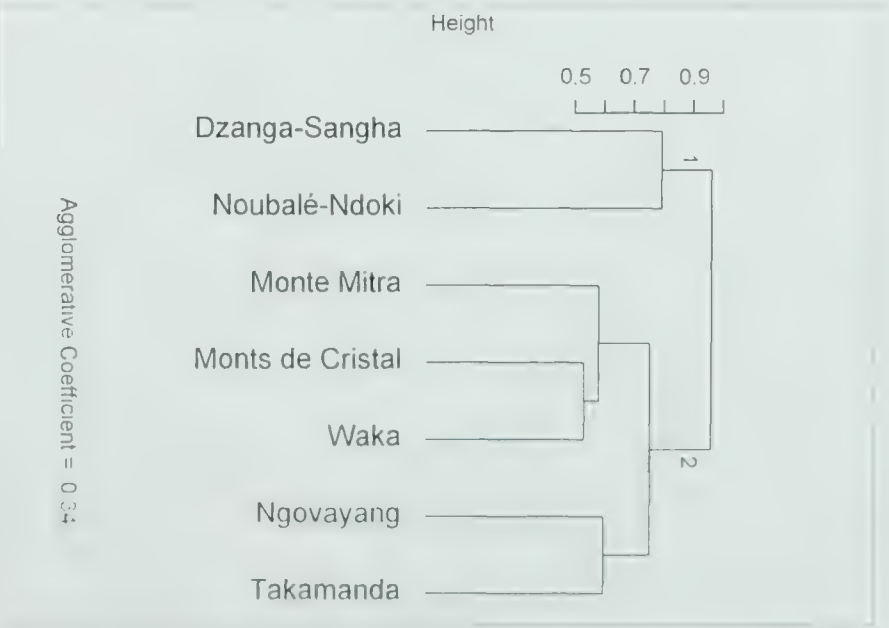


Figure 2 – Distances écologiques (Bray-Curtis binaire) entre les sites en Afrique Centrale sur la base des listes d'espèces. Le chiffre 1 représente les sites continentaux, et le chiffre 2 correspond aux sites côtiers.

(forêts continentales vs forêts côtières), avec la même subdivision parmi les forêts périphériques au golfe de Guinée (fig. 3). Les indices de dissimilarité de Bray-Curtis sont globalement plus faibles, avec des valeurs inférieures à 50%. Ces faibles distances traduisent une plus grande similarité floristique au niveau taxonomique des familles.

DISCUSSION

Analyse phytogéographique du massif de Ngovayang

Les proportions d'espèces guinéo-congolaises (79%) et de liaison (10%) du massif de Ngovayang sont remarquablement proches de celles avancées par White (1983) pour l'ensemble de la région phytogéographique. Cet auteur affirme que la flore guinéo-congolaise dans son ensemble est remarquablement pure, avec plus de 80% d'endémiques et seulement 10% environ d'espèces de liaison. Cette prédominance d'espèces guinéo-congolaises dans les parcelles étudiées est largement imputable au fait que nous avons sélectionné des parcelles de forêts matures, peu ou pas perturbées par les activités humaines. Des résultats similaires ont été obtenus pour la flore du Kasai, en République Démocratique du Congo (Lubini 2001) et pour la flore du centre du Gabon (Doucet 2003), avec respectivement 79% et 81% d'espèces guinéo-congolaises.

Par ailleurs, la présence d'espèces appartenant aux familles des Huaceae, Hoplestigmataceae, Medusandraceae, Lepidobotryaceae, Octoknemaceae, et Scytropetalaceae, familles strictement liées au centre régional d'endémisme guinéo-congolais (White 1983), permet de rattacher sans ambiguïté le massif de Ngovayang à ce fond floristique. Les forêts de basse et moyenne altitudes du massif comprennent 81,5% des familles (31 familles sur 38) et 39% de genres (19 genres sur 49) cités par White (1983) comme endémiques de ce centre régional d'endémisme.

La prédominance des espèces du domaine guinéen inférieur (tableau 1) dans la flore du massif de Ngovayang montre que ce dernier appartient bien au domaine guinéen

inférieur tel que défini par Aubréville (1962) et White (1979). Ce secteur phytogéographique est particulièrement soumis à la mousson atlantique ainsi que, dans sa partie sud, à l'effet refroidissant du courant du Benguela qui assure une humidité atmosphérique importante même en saison sèche (Suchel 1972, White 1983). Ce climat, favorable au développement des forêts denses sempervirentes, a pu perdurer par le passé et favoriser le développement et l'extension d'espèces caractéristiques sur l'ensemble de ce secteur bas-guinéen (Maley & Brenac 1998). C'est le cas, par exemple, des Leguminosae-Caesalpinioideae. Plus de 40% des Leguminosae-Caesalpinioideae recensées à Ngovayang appartiennent au domaine guinéen inférieur (fig. 4). Parmi ces espèces, certaines ont été identifiées comme bio-indicatrices de forêts anciennes, voire de refuges forestiers, dans la région de Campo Ma'an, à environ 75 km au sud de Ngovayang (fig. 1; Tchouto et al. 2009). Il s'agit de *Berlinia craibiana*, *B. auriculata*, *Gilbertiodendron ogoouense*, *Guibourtia tessmannii*, *Amphimas ferrugineus*, *Plagiosiphon longitubus* et *Leonardoxa africana* subsp. *gracilicaulis*.

Les Leguminosae-Caesalpinioideae grégaires sont bien représentées dans tout le domaine guinéen inférieur, en particulier les espèces dont les mécanismes de dispersion (barochore et autochore) ne permettent pas une dispersion rapide à grande distance. C'est le cas, par exemple, des forêts de Korup (Newbery et al. 2004), de Campo-Ma'an (Tchouto et al. 2009), et de Ngovayang (Gonmadje et al. 2011). Seul le maintien de conditions favorables pendant des périodes longues peut expliquer leur répartition dans toute la région. Parmi ces espèces, on peut citer *Tetraberlinia bifoliolata*, *Guibourtia tessmannii* et *Didelotia letouzeyi*, qui dominent les forêts de Ngovayang et sont marqueurs des forêts sempervirentes côtières (Vivien & Faure 1985, Wieringa 1999, Doucet 2003). Ainsi, la dominance des Leguminosae-Caesalpinioideae confirme l'appartenance du massif de Ngovayang au "district atlantique biafréen riche en Caesalpinaceae" tel que défini par Letouzey (1968, 1985) sur des caractères qualitatifs (listes d'espèces) ou semi-quantitatifs (estimation à vue du gréganisme des espèces).

En revanche, les espèces à large distribution, qui illustrent le caractère secondaire ou de substitution d'un site donné consécutivement aux activités humaines (Evrard 1968, Habiyaemye 1997), sont faiblement représentées dans les forêts non perturbées de Ngovayang (2% des espèces). Cela confirme la maturité des peuplements étudiés. Nos relevés, bien que ne renfermant que très peu d'espèces de végétation secondaire, restent parmi les plus riches des forêts de la région (Gonmadje et al. 2011).

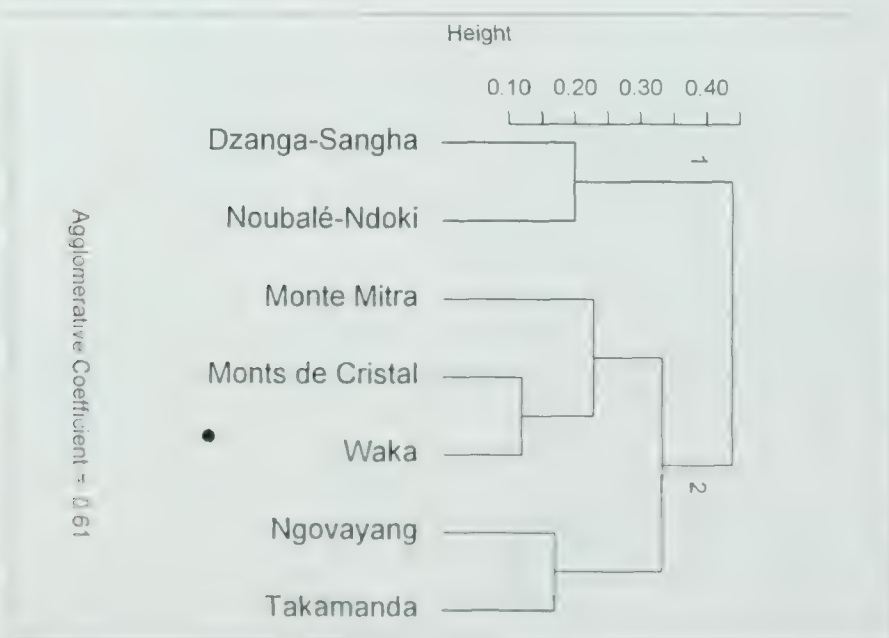


Figure 3 – Distances écologiques (Bray-Curtis binaire) entre les sites en Afrique Centrale sur la base des listes de familles. Le chiffre 1 représente les sites continentaux, et le chiffre 2 correspond aux sites côtiers.

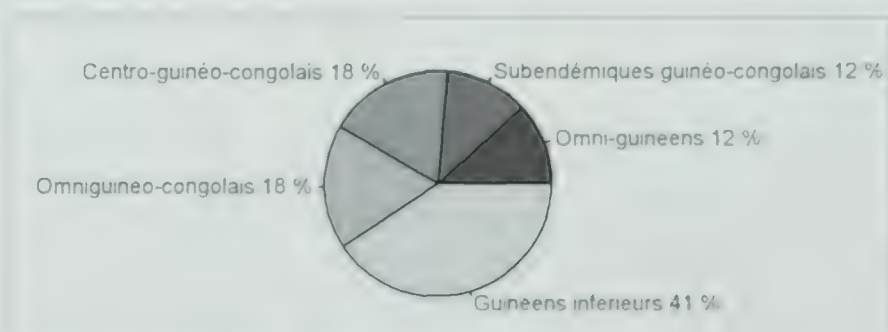


Figure 4 – Types phytogéographiques des Leguminosae-Caesalpinioideae inventoriées dans le massif de Ngovayang.

Dissimilarités floristiques entre les sites côtiers et continentaux

L'analyse phytogéographique des différents sites étudiés confirme l'originalité floristique des forêts situées sur le pourtour du golfe de Guinée comparativement à celles de l'intérieur du continent, y compris celles situées en marge de la Cuvette congolaise, comme Nouabalé-Ndoki et Dzanga-Sangha. Ces résultats corroborent ceux d'Aubréville (1962), Letouzey (1968, 1985), White (1983), Senterre (2005) et Droissart (2009). Sur ces sites continentaux on constate, par exemple, une forte régression des Burseraceae et des Olacaceae (Senterre & Nguema 2001, Sonké 2005, Sunderland & Balinga 2005, Balinga et al. 2006).

Les différences climatiques présentes ou passées pourraient expliquer cette différenciation floristique ouest-est. Les sites côtiers, sous l'influence de la mousson atlantique, sont caractérisés par de fortes précipitations (≥ 2000 mm/an), une forte nébulosité et une saison sèche moins marquée (1–3 mois). En revanche, les sites continentaux sont déterminés par des précipitations plus faibles (1400–1700 mm/an) et une saison sèche plus longue (1–4 mois) et plus sévère, notamment en périphérie de la cuvette congolaise (Suchel 1972, White 1983). Les variations passées du climat ont aussi été probablement plus importantes pour Nouabalé-Ndoki et Dzanga-Sangha que pour les sites côtiers (Maley 2002). En effet, ces deux sites sont situés dans le corridor de la Sangha, une zone connue pour avoir subi une ouverture de la forêt et une extension de la savane durant les phases climatiques arides passées (White 1979).

D'autres facteurs, tels que le sol ou d'anciens impacts humains pourraient aussi expliquer ces différences floristiques (Boulvert 1986, Sheil 2001, Tuomisto et al. 2003, Réjou-Méchain et al. 2008). Ce dernier facteur a été minimisé autant que possible en écartant de nos analyses les parcelles inventoriées dans des forêts perturbées. Concernant le facteur sol, les parcelles sur sol inondable ou à nappe phréatique proche de la surface ont été écartées mais, il est possible que des différences dans la teneur en sable des parcelles de Nouabalé-Ndoki et Dzanga-Sangha (Boulvert 1983) puissent expliquer une partie de leur dissimilarité floristique relativement aux sites atlantiques, tous situés sur des sols nettement argileux. En l'absence de données précises sur les sols de ces sites, il nous est impossible d'en tirer une conclusion fiable. La multiplication de comparaisons de parcelles et des analyses plus fines intégrant la composition des sols seront nécessaires afin d'affiner notre compréhension des facteurs de variations biogéographiques sur toute la région.

Affinités et dissimilarités floristiques entre les sites côtiers

Les forêts côtières ou atlantiques ont en commun, parmi les taxa dominants, la sous-famille des Leguminosae-Caesalpinioideae et, les familles des Olacaceae, des Euphorbiaceae, des Clusiaceae, des Burseraceae, des Annonaceae et des Rubiaceae (Sunderland et al. 2003, 2004, Balinga et al. 2005, Balinga 2006, Gonmadje et al. 2011). Ceci expliquerait en partie la forte similarité floristique observée entre ces sites côtiers au niveau familial. L'importance des Leguminosae-Caesalpinioideae, en particulier les espèces grégaires, permet

de rassembler ces forêts dans un même domaine phytogéographique: le domaine guinéen inférieur. Toutefois, des différences de composition floristique, tant au niveau spécifique que familial, ont permis d'identifier deux groupes de sites, Takamanda et Ngovayang d'une part, et les autres sites côtiers de l'autre (figs 2 & 3).

Contrairement à l'une des hypothèses émises au début de cet article, les forêts de Ngovayang ont ainsi plus d'affinités avec celles de Takamanda qu'avec les autres forêts bordant, au Sud, l'océan Atlantique. La présence de la LVC et du fleuve Sanaga semble jouer un rôle moins important dans la structuration phytogéographique des forêts de basse et moyenne altitude de Basse-Guinée que la 'charnière climatique' qui marque le passage du régime climatique boréal au régime austral (Suchel 1990, Thomas & Goudie 2000); cette charnière climatique étant située au Sud du Cameroun, vers la frontière avec la Guinée-Equatoriale (fig. 1). De nombreux travaux ont montré que certains fleuves (Sanaga, Cross, Congo) jouent un rôle important de barrière géographique dans la structuration de la biodiversité animale; c'est le cas pour le Bonobo (Ericksson et al. 2004), le Gorille (Anthony et al. 2007) et d'autres primates (Colyn et al. 1991). Concernant la végétation, ce rôle de barrière de dispersion est beaucoup plus rarement évoqué que dans le règne animal mais pourrait toutefois fonctionner pour certaines espèces telles que *Garcinia preussii* (Clusiaceae) et *Psorospermum membranaceum* (Hypericaceae; Cheek et al. 2001), les genres *Diospyros* (White 1978) ou *Begonia* (Sosef 1994), et pour les Orchidaceae (Droissart 2009). Il ne semble toutefois pas s'appliquer aux peuplements d'arbres que nous avons étudiés.

Le massif de Ngovayang est géographiquement plus proche de Monte Mitra et des monts de Cristal que de Takamanda (fig. 1). Par ailleurs, la réserve de Takamanda est géographiquement plus proche de la LVC que du massif de Ngovayang. Certaines espèces de montagne, issues d'un fond floristique original et présentant des affinités avec l'Afrique orientale, auraient pu donner naissance à des formes de basse et moyenne altitude (White 1987), favorisant l'originalité du peuplement forestier de Takamanda. Mais ce mécanisme potentiel ne semble pas avoir fonctionné de cette manière, tout au moins concernant le peuplement des arbres. La réserve de Takamanda, située à la frontière nigéro-camerounaise, présenterait des affinités floristiques plus importantes avec les forêts du sud-est du Nigéria (White 1979, Letouzey 1985). Cependant, nos résultats montrent que, malgré la distance géographique qui les sépare, ainsi que leur position opposée vis-à-vis de la LVC et du fleuve Sanaga, Ngovayang et Takamanda sont floristiquement plus proches entre eux qu'ils ne le sont des forêts situées au sud de la charnière climatique (Monte Mitra, monts de Cristal, Waka). Le massif de Ngovayang constituerait alors une zone de transition floristique entre les forêts du Nigéria et celles s'étendant du sud-ouest Cameroun jusqu'en RDC.

La charnière climatique évoquée ci-dessus est le reflet du décalage des saisons entre les deux régimes climatiques boréal et austral. En réduisant le succès de la pollinisation (phénologie de floraison décalée) ou de l'établissement des plantules (dispersion et germination des graines hors la saison optimale), ce décalage pourrait compliquer, après une

péjoration climatique, la recolonisation par certaines espèces forestières adaptées à l'un ou l'autre climat. L'hétérogénéité floristique observée au sein des sites côtiers serait due non seulement à la présence actuelle de cette charnière climatique mais aussi aux variations climatiques passées (Maley 1996, Plana et al. 2004). L'impact de ces fragmentations, en particulier celles du Pléistocène et de l'Holocène, a été conditionné par les réponses des différentes espèces à cette charnière climatique, qui peut ainsi favoriser la rémanence de ces anciennes fragmentations. Ceci pourrait expliquer la dissimilarité floristique existante entre les forêts de Ngovayang et de Takamanda avec celles situées plus au Sud, suggérant l'existence des deux entités phytogéographiques au sein du domaine de Basse-Guinée. Ces termes de charnière climatique (*climatic hinge* en anglais), bien que peu usités, matérialisent la ligne imaginaire qui coupe la zone tropicale en séparant les régions recevant l'essentiel des précipitations au cours de l'été boréal de celles qui sont affectées par les pluies d'été de l'hémisphère austral (Thomas & Goudie 2000). Suchel (1990) a utilisé l'expression "ligne de démarcation du passage du régime boréal au régime austral" pour matérialiser cette zone de basculement climatique. Nous suivrons ainsi les appellations de ces deux auteurs, en évitant d'introduire dans le texte des termes qui – s'ils s'avèrent pratiques à utiliser – n'en sont pas moins sources de confusions. En effet, par assimilation à l'équateur géographique (cercle terrestre de latitude 0°), les termes d' "équateur climatique" ou "équateur thermique" ont été utilisés par plusieurs auteurs (Daïnou et al. 2010, Debout et al. 2011, Duminil et al. 2010), pour qualifier cette charnière climatique. L' "équateur thermique" est la zone des plus hautes températures moyennes autour de la terre, dont la position peut varier selon les époques mais qui a été situé, sur le long terme, à près de 5° de latitude Nord, au nord de la zone de basculement climatique à laquelle nous faisons référence (Allaby & Allaby 1999). L' "équateur climatique" correspond quant à lui à une ligne imaginaire où se rencontrent les masses d'air boréale et australe; cet équateur climatique varie au cours des saisons en fonction du balancement de la zone de convergence intertropicale (ZCIT). Si ces positions extrêmes sont mentionnées dans les travaux consultés (Beltrando & Camberlin 1993, Allaby & Allaby 1999, Kaser 1999), l'équateur climatique n'est jamais matérialisé par une ligne précise. Ce terme pourrait être pratique mais il s'avère finalement inadapté à rendre compte de la réalité géographique du basculement des saisons entre les deux hémisphères.

A l'échelle régionale, Balas et al. (2007) ont montré que la région du Sud-Cameroun, et celle formée par la Guinée-Equatoriale et le Gabon, sont deux régions climatiques bien distinctes, chacune étant homogène en termes de variabilité interannuelle des précipitations, de saisons humide et sèche principales. Au nord, la saison sèche principale est centrée sur décembre-février, avec des précipitations importantes en été boréal. Au sud de cette charnière climatique, la saison sèche principale se situe en juin-août; un creux de précipitation est plus ou moins marqué en hiver boréal mais les pluies restent toujours relativement importantes. Par ailleurs, Suchel (1990) a bien mis en évidence de manière détaillée le phénomène d'inversion des saisons sèches dans le sud-ouest du Cameroun. Le passage du régime boréal au

régime austral, encore discret sur le territoire camerounais, devient plus visible un peu plus au sud de Ngovayang, en bordure de l'océan, notamment au sud de Campo, et s'étend en Guinée-Equatoriale et au Gabon. D'autres paramètres climatiques, plus discrets que la pluviométrie, ont aussi révélé un contraste Nord/Sud. Il s'agit des moyennes des températures minimales journalières, de l'humidité relative et de l'évaporation. D'après Suchel (1990), la ligne de démarcation du passage au véritable régime austral, située à environ 2°0'N, écorne l'angle sud-ouest du territoire camerounais (fig. 1).

D'autres paramètres importants pour la végétation différencient les climats observés au nord et au sud de cette charnière climatique. L'harmattan, un vent desséchant soufflant du nord-est en provenance du Sahara, atteint parfois la zone des forêts ombrophiles situées au nord de la charnière climatique mais ne pénètre pas dans les forêts du Sud. Au Ghana, par exemple, lorsque l'harmattan souffle, l'humidité relative peut tomber jusqu'à 53% (White 1983). Le climat de l'hémisphère Nord est donc caractérisé par une saison sèche principale plus sévère, plus ensoleillée et plus sèche que celle du Sud (Suchel 1972, 1990, Saint-Vil 1984). La principale saison sèche australe est caractérisée quant à elle par une couverture nuageuse stratiforme – due à l'effet refroidissant du courant du Benguela – qui provoque une diminution des températures, limite l'évapo-transpiration et favorise les brouillards matinaux (Saint-Vil 1984, Suchel 1990, Fontaine & Bigot 1993, Wotling et al. 1995, Bigot et al. 1997, Balas et al. 2007). Le climat y reste relativement humide et donc favorable à la survie des végétaux, même si les précipitations annuelles sont moins importantes qu'autour de la LVC.

Par ailleurs, plusieurs climatologues et palynologues (Bond et al. 1997, deMenocal et al. 2000, Leuschner & Sirocko 2000, Maley 2002, Giresse et al. 2005) ont pu reconstituer les principales variations de la position de la charnière climatique durant l'Holocène, qui se situait plus au nord qu'actuellement, suggérant une remontée vers le nord de celle-ci. Au niveau du Cameroun, au cours de l'Holocène inférieur et moyen, la limite nord de la forêt dense se situait sur le rebord septentrional du plateau de l'Adamaoua. L'aire de distribution d'*Aucoumea klaineana*, dont la limite nord actuelle correspond à la charnière climatique, s'étendait durant l'Holocène inférieur et moyen jusqu'au bord du lac Ossa, 170 km au nord de sa limite actuelle (Reynaud-Farrera 1995). Le recul d'*Aucoumea klaineana* vers le Sud serait associé à la phase de péjoration climatique intervenue entre 2500 et 2000 BP. Le positionnement actuel de la charnière climatique daterait de l'Holocène récent (Bond et al. 1997, deMenocal et al. 2000, Leuschner & Sirocko 2000, Maley 2002, Giresse et al. 2005). Le phénomène d'inversion des saisons et la présence d'une saison sèche plus drastique dans l'hémisphère Nord et l'histoire climatique passée dont il a été fait mention pourraient ainsi être la cause de la limitation à la dispersion de certaines espèces du Sud vers le Nord telle que *Aucoumea klaineana* (Muloko 2001, Born 2007), ou de différences génétiques au sein d'une même espèce: c'est le cas d'*Irvingia gabonensis* (Irvingiaceae; Lowe et al. 2010), *Milicia excelsa* (Moraceae; Daïnou et al. 2010) et *Distemonanthus benthamianus* (Léguminosae-Caesalpinioideae; Debout et al. 2011).

Outre les Leguminosae-Caesalpinioideae, d'autres familles telles que les Olacaceae et les Burseraceae caractériseraient les forêts atlantiques matures (Doumenge 1992, Senterre & Lejoly 2001, Doucet 2003), bien que leur importance soit variable en fonction des forêts considérées. C'est le cas des Burseraceae, qui sont moins importantes (en termes de FIV) dans les forêts camerounaises que dans celles de Guinée-Equatoriale, du Gabon ou du Congo (Doumenge 1992, Senterre & Nguema 2001, Doucet 2003). En effet, les aires de répartition de plusieurs Burseraceae forestières sont, soit limitées au sud de l'équateur thermique, en climat d'hémisphère Sud, soit ne l'atteignent ou ne le dépassent que très marginalement, au Sud-Cameroun. C'est le cas d'*Aucoumea klaineana* et de diverses espèces de *Dacryodes*. Même parmi les Leguminosae-Caesalpinioideae, certaines espèces sont limitées au sud de la charnière climatique (*Anthonothea ferruginea*, *A. mouandzae*, *A. pellegrinii*, *A. stipulacea*, *A. trunciflora*) et d'autres au Nord (*Anthonothea wijmacampensis* et *A. xanderi*; Breteler 2010).

Bien que Droissart (2009) ait considéré la chaîne Ngovayang-Mayombe (Cameroun-RDC) comme une seule aire d'endémisme morcelée pour la distribution des Orchidaceae en Afrique Centrale, ses travaux ont aussi révélé, au sein des sites côtiers de Basse-Guinée qu'il a étudiés, l'existence de deux ensembles phytogéographiques qui corroborent nos résultats: un groupe formé par Ngovayang et Campo d'une part, et un autre formé par les monts de Cristal, le Monte Alen et le massif du Chaillu d'autre part. Même si l'auteur n'a pas expliqué l'existence de ces deux entités phytogéographiques, les différences constatées pourraient être liées à l'influence de la charnière climatique nord-sud.

Au total, et même si les mécanismes biologiques de différenciation floristique nord-sud ne sont pas encore totalement élucidés, l'importance de cette charnière climatique dans la structuration de la biodiversité végétale apparaît comme un élément de la biogéographie des forêts denses humides africaines qui a été par trop négligé jusqu'à présent. Nos propres données, combinées aux résultats présentés sur d'autres groupes biologiques (herbacées, arbustes) et à d'autres échelles taxonomiques (phylogéographie intraspécifique), fournissent ainsi des pistes pour la réinterprétation phytogéographique du domaine bas-guinéen.

CONCLUSION

Les forêts de basse et moyenne altitude du massif de Ngovayang présentent une composition floristique caractéristique de forêts atlantiques matures riches en Leguminosae-Caesalpinioideae grégaires, typiques du domaine floristique bas-guinéen. Ce massif constitue une zone de transition entre l'ensemble des forêts périphériques aux reliefs de la LVC et l'archipel de petits sommets qui bordent l'océan Atlantique jusqu'à la RDC. Cependant, le massif de Ngovayang semble floristiquement plus proche des forêts de basse et moyenne altitude Camerouno-nigériane que de celles de la Guinée Equatoriale et du Gabon. Il semble donc, comme cela a aussi été démontré par des travaux de phylogéographie, que la présence de la charnière climatique, aux confins camerouno-gabonais, ait constitué une barrière climatique suffisante

pour permettre la différenciation d'assemblages floristiques particuliers au nord et au sud de cette limite.

Des études plus poussées sont toutefois nécessaires afin de préciser si ce schéma identifié sur les peuplements d'arbres des forêts de basse et moyenne altitude se confirme pour d'autres types biologiques (arbustes, lianes, épiphytes) et d'autres types forestiers, en particulier les forêts submontagnardes. Enfin, il sera nécessaire de compléter non seulement les inventaires sur les sites présentés ici, mais aussi de compléter l'échantillonnage par des inventaires similaires dans d'autres sites, permettant de mieux couvrir la variabilité des forêts du domaine guinéen inférieur. Ces données permettront d'apporter plus de précisions sur la phytogéographie et l'histoire de ces forêts, fournissant des informations nécessaires aux politiques et aux gestionnaires pour la mise en place des stratégies de conservation et de gestion des ressources forestières efficaces à l'échelle nationale, voire sous-régionale. Elles pourront également permettre le développement d'une meilleure compréhension de la paléo-histoire des forêts de cette partie du continent.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible au format pdf sur *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), et comprend: (1) une liste des espèces d'arbres inventoriées et identifiées jusqu'au niveau spécifique dans le massif de Ngovayang; (2) une liste des espèces citées dans le texte, et absentes du massif de Ngovayang; et (3) les formules de calcul de l'*Importance Value Index* (IVI; Curtis & McIntosh 1951), du *Family Importance Value Index* (FIV; Mori et al. 1983) et de l'indice de dissimilarité de Bray-Curtis binaire (BC_{ij}).

REMERCIEMENTS

Nous remercions le projet "Sud Expert Plantes" (SEP) financé par le Ministère français des Affaires Etrangères et Européennes, et le Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD) pour avoir financé ce travail. Nous remercions aussi N. Fauvet, du CIRAD, pour son assistance technique dans la cartographie. Nous ne manquerons pas de témoigner notre reconnaissance envers M. Sainge, P. Mezili and J.-M. Onana pour leur expertise dans l'identification des échantillons aussi bien sur le terrain qu'à l'Herbier National du Cameroun. Nous remercions également V. Freycon, D. McKey, J. Maley, B. Sinsin et les trois relecteurs anonymes pour leurs critiques et suggestions qui ont permis d'améliorer la qualité de ce travail. Nous ne saurions terminer sans remercier les populations locales du massif de Ngovayang qui ont contribué à la collecte des données sur le terrain.

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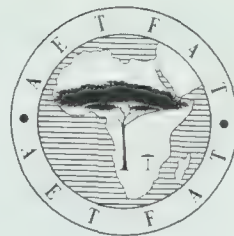
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Manuscript received 29 Oct. 2010; accepted in revised version 23 Feb. 2012. This paper was pre-published on 6 Jul. 2012 in issue 145(2) of *Plant Ecology and Evolution*.

Communicating Editor: Porter P. Lowry II.



Groupements végétaux de la région de la Loky-Manambato (Daraina, Nord-Est de Madagascar): caractéristiques floristiques et phytogéographie

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Vegetation associations in the Loky-Manambato region (Daraina, North-East Madagascar): floristic characteristics and phytogeography

Background and aims – The vegetation of the Loky-Manambato region is influenced by strong gradients in precipitation, temperature and altitude. The aim of this contribution is to characterize the floristic features of the area by studying forest vegetation associations and to analyse their relationships with the phytogeographical Domains of Madagascar.

Methods – The vegetation has been studied by 101 linear relevés each 100 m in length. Similarity between the relevés (using the Horn similarity index), based on species frequencies, was used to develop a classification (using Ascendant Hierarchical Classification methods) of distinct vegetation groups, each characterized by indicator species. Knowing the distribution of these species, it was then possible to detail the phytogeographical affinities of each group.

Key Results – Twelve main vegetation associations were identified. The phytogeographical affinities revealed are not just limited to the Western Domain, but also the Eastern, Sambirano and Central Domains. Altitude appears to have a primary influence.

Conclusion – Results provide a better understanding of the entanglement of floristic Domains with respect to site-level environmental conditions in cases where a transitional region is analysed at a fine scale. They confirm the key role of the Loky-Manambato region in understanding the biogeography of northern Madagascar.

Key words – Vegetation, biogeography, Loky-Manambato, Madagascar, linear relevé.

Objectif – La végétation de la région Loky-Manambato est conditionnée par de forts gradients de précipitation, de température et d'altitude. L'objectif de ce travail consiste à caractériser les particularités floristiques de la région au travers des groupements forestiers végétaux et de leurs espèces caractéristiques afin d'évaluer leurs relations avec les Domaines Phytogéographiques à l'échelle de Madagascar.

Méthodes – La végétation a été étudiée par 101 relevés linéaires de 100 m de longueur. La mesure de la similarité entre les relevés (indice de similarité de Horn) calculée à partir des fréquences des espèces a permis de réaliser une classification (Classification Ascendante Hiérarchique) des groupements végétaux distincts. Chacun est caractérisé par des espèces indicatrices. Connaissant la distribution de ces espèces, il devient possible de préciser les affinités phytogéographiques de ces groupements.

Résultats – Douze principaux groupements végétaux ont été identifiés. Les affinités phytogéographiques qui ressortent sont non seulement avec le Domaine de l'Ouest, mais également de l'Est, du Sambirano et du Centre. L'influence de l'altitude apparaît prépondérante.

Conclusion – Les résultats permettent de mieux comprendre l'intrication des Domaines floristiques en fonction des conditions stationnelles lorsqu'une région de transition est analysée à une échelle fine. Ils confirment le rôle majeur de la région Loky-Manambato dans la compréhension de la biogéographie du Nord de Madagascar.

INTRODUCTION

Depuis la découverte d'une nouvelle espèce de lémurien (*Propithecus tattersalli*) vers les années 1980 dans la zone de Loky-Manambato au Nord-Est de Madagascar (Simons 1988), des recherches dans divers domaines, dont la flore et la végétation, se sont succédé dans cette région et aboutissent à des résultats importants pour la compréhension de la biogéographie du Nord de Madagascar, ainsi qu'en termes de conservation.

Cette région est comprise entre les latitudes 12°45'S et 13°20'S et les longitudes 49°25'E et 49°55'E dans la Région SAVA (sous-préfecture de Vohémar). Elle couvre une superficie d'environ 250000 ha. Une quinzaine de massifs forestiers y subsistent, au sein de zones déforestées de longue date.

La particularité de cette région tient principalement dans sa position géographique aux confins des quatre principaux Domaines phytogéographiques de Madagascar: Est, Centre, Ouest et le Sambirano (Humbert 1955). Même si la région Loky-Manambato est située globalement dans le secteur Nord du Domaine de l'Ouest, l'altitude de certains massifs culminant à plus de 1000 mètres a localement une forte influence sur la température et l'humidité créant par endroit des conditions écologiques comparables à celles rencontrées dans les Domaines de l'Est du Sambirano ou du Centre (Gautier et al. 2006).

Dans une précédente contribution (Ranirison et al. 2010) nous avons étudié la relation entre les facteurs environnementaux et la répartition des groupements végétaux dans la région Loky-Manambato. Le présent travail a pour but d'analyser l'affinité de ces groupements végétaux avec les domaines phytogéographiques de l'île.

MATERIEL ET METHODES

Le présent travail est basé sur les mêmes données que celles analysées dans un précédent article (Ranirison et al. 2010). Cent-un relevés de végétation ont été effectués au cours de 309 jours de terrain, de 2004 à 2006. Ces relevés ont été réalisés dans les 10 principaux blocs forestiers de la région avec 8 à 12 relevés par bloc, selon la taille du bloc de manière à toucher le plus grand nombre d'unités de végétation. L'échantillonnage stratifié a été adopté pour repérer les zones de végétation similaires qui ont été obtenues par superposition de différentes cartes (topographique, géologique et pédologique) ainsi que par utilisation de photos aériennes et d'images satellites de la région. La méthode de relevé employée (Gautier et al. 1994) consiste à faire des observations tous les 2 m le long d'une ligne de 100 m dans une zone de végétation jugée homogène sur le terrain. A chaque point de mesure, les contacts avec la végétation à la verticale du

point de mesure sont notés (espèce et hauteur du contact). Les paramètres environnementaux tels que l'altitude, la pente, l'orientation et le substrat ont également été enregistrés pour chaque relevé. Les espèces rencontrées dans les relevés ont fait l'objet de collecte d'échantillons qui ont été identifiés dans les herbiers aussi bien nationaux (TAN et TEF) qu'internationaux (G, P et envoi de doubles aux taxonomistes spécialisés dans 26 institutions). Cette méthode a été largement utilisée à Madagascar dans divers travaux d'inventaires forestiers (Birkinshaw et al. 1998, Messmer & Rakotomalaza 1999, Messmer et al. 2000, 2002, Ramandimbimanana 2009, Razanajatovo 2009, Madiomanana 2010, Ranirison 2010, Tahinarivony 2010) ainsi que dans d'autres forêts intertropicales (Chatelain 1996, Bakayoko 1999, 2005, Brockelmann 1998, Bakayoko et al. 2005, Nusbaumer et al. 2005).

Pour bien mettre en exergue l'aspect floristique vu qu'il s'agit d'une analyse phytogéographique, la classification des groupements végétaux s'est basée sur la fréquence des espèces de chaque relevé.

Les données issues des relevés de végétation ont été traitées en utilisant le progiciel "R" (Legendre & Vaudor 1991). Le calcul de l'indice de similarité *Ro* de Horn (Horn 1966) qui se base sur la présence ainsi que la fréquence des espèces rencontrées a été choisi pour obtenir une matrice de dissimilarité des relevés. Par la suite, un dendrogramme a été généré par agrégation de ces relevés suivant la méthode 'Unweighted Pair Group Method with Arithmetic mean' (UPGMA, Oppenheimer 1997). Les groupements qui en découlent sont ensuite traités par le logiciel IndVal qui permet d'identifier les espèces dont l'abondance relative et la fréquence relative sont supérieures ou égale à 50%: ce sont les espèces indicatrices de chacun de ces groupements (Dufrêne & Legendre 1997). La distribution géographique de ces espèces indicatrices a été obtenue par les informations contenues dans la Flore de Madagascar (Humbert 1936), des inventaires régionaux (Gautier 2002, Trigui 2010) ainsi qu'en consultant les bases de données en ligne telles que Tropicos (<http://www.tropicos.org>), Sonnerat (<http://coldb.mnhn.fr/colweb>). En fonction de leur présence dans les différents domaines phytogéographiques de Humbert (1955) (W; Sb; E; C; S) ces espèces sont rattachées à différentes catégories phytogéographiques (E; E-Sb; E-Sb-W; etc.). Chaque groupement végétal est donc caractérisé par une liste d'espèces indicatrices, chacune attribuée à une catégorie phytogéographique. Pour chaque groupement végétal, le rapport entre le nombre d'espèces indicatrices appartenant à une catégorie phytogéographique et le nombre total d'espèces indicatrices donne le pourcentage de cette catégorie phytogéographique. On peut ensuite analyser la variation de ces pourcentages en fonction de l'altitude.

Tableau 1 – Affinité phytogéographique et répartition altitudinale des groupements végétaux.
E: Domaine de l’Est; C: Domaine du Centre; C, E: espèces présentent dans conjointement dans les Domaines de l’Est et du Centre; W: Domaine de l’Ouest. Les valeurs des catégories phytogéographiques supérieures à 20% ainsi que les deux plus grandes valeurs sont mises en évidence en gras. Pour l’altitude, les deux valeurs extrêmes minimales et maximales sont affichées ainsi que l’altitude moyenne, mis entre parenthèses.

Groupes floristiques	E	C	C, E	W	Altitude (m)
Groupement à <i>Kosteletzkya retrobracteata</i> et <i>Phyllarthron bernierianum</i> (G11)	< 3	< 3	< 3	40,0	65 à 118 (91)
Groupement à <i>Wielandia fadenii</i> et <i>Helmiopsis inversa</i> (G6)	3,7	< 3	3,7	40,7	180 à 220 (200)
Groupement à <i>Xyloolaena perrieri</i> et <i>Diospyros haplostylis</i> var. <i>hildebrandtii</i> (G1)	9,4	< 3	6,3	31,3	210 à 315 (262)
Groupement à <i>Uncarina peltata</i> et <i>Stereospermum hildebrandtii</i> (G10)	< 3	< 3	< 3	85,7	120 à 520 (320)
Groupement à <i>Mallotus oppositifolius</i> et <i>Drypetes</i> aff. <i>Thouarsii</i> (G8)	10,0	< 3	< 3	30,0	160 à 525 (342)
Groupement à <i>Perrierbambus</i> cf. <i>madagascariensis</i> et <i>Noronhia crassinodis</i> (G12)	13,3	< 3	6,7	33,4	140 à 580 (360)
Groupement à <i>Cynometra commersoniana</i> et <i>Homalium albiflorum</i> (G7)	30,0	< 3	< 3	60,0	135 à 600 (367)
Groupement à <i>Vepris nitida</i> et <i>Rinorea angustifolia</i> (G9)	18,2	< 3	27,3	18,2	285 à 578 (431)
Groupement à <i>Trophis montana</i> et <i>Trichilia cauliflora</i> (G2)	15,4	< 3	< 3	7,7	310 à 830 (570)
Groupement à <i>Tina striata</i> subsp. <i>multifoliolata</i> et <i>Tabernaemontana ciliata</i> (G3)	10,0	9,0	50,0	10,0	285 à 850 (680)
Groupement à <i>Asplenium nidus</i> et <i>Dypsis nodifera</i> (G4)	23,3	< 3	26,7	6,6	800 à 1040 (920)
Groupement à <i>Uapaca densifolia</i> et <i>Macaranga obovata</i> (G5)	23,5	20,6	35,3	< 3	860 à 1065 (962)

RESULTATS

Après analyse et traitement des données issues de ces 101 relevés linéaires, douze groupements végétaux ont été mis en évidence dans la région Loky-Manambato (G1 à G12). Les pourcentages d’attribution des espèces indicatrices aux catégories phytogéographiques de chaque groupement végétal sont résumés dans le tableau 1 (liste des espèces indicatrices par groupe en appendice électronique). Ne sont représentés dans ce tableau que les catégories phytogéographiques dont au moins l’un des pourcentages dépasse la valeur de 20%. Les catégories phytogéographiques généralistes comme W-Sb-E-C-S ou Sb-E-C n’y sont pas représentées car elles présentent des pourcentages très faibles du fait que les espèces présentant de telles distributions ne ressortent en général pas comme espèces différentielles marqueurs d’un groupe. Les catégories les plus fréquentes sont en fait au nombre de quatre: E, C, C-E, W.

D’après ce tableau, les trois grands domaines phytogéographiques de l’Est, de l’Ouest et du Centre sont largement majoritaires. La figure 1 montre en détail l’histogramme cumulé de la valeur du pourcentage de l’appartenance phytogéographique des groupements respectifs. La valeur des groupements affins au Domaine de l’Ouest (W) diminue progressivement quand l’altitude croît. Pour les groupements du

Domaine de l’Est et du Centre, cette valeur augmente significativement avec l’altitude.

La succession des Domaines phytogéographiques dans la zone suit l’altitude:

- groupements à affinité avec le Domaine de l’Ouest localisés aux altitudes inférieures (≤ 600 m);
- groupements à affinité avec le Domaine de l’Est localisés aux altitudes intermédiaires (285 à 920 m);
- groupements à affinité avec le Domaine du Centre localisés aux altitudes supérieures (≥ 800 m).

DISCUSSION

Dans une première analyse menée sur les mêmes données (Ranirison et al. 2010), dix groupements végétaux avaient été identifiés. L’analyse présentée ici a conservé huit de ces groupements, les relevés restants étant partagés en quatre groupements au lieu de deux. Par opposition au recouvrement utilisé auparavant, le présent travail a opté sur la fréquence pour la classification des relevés.

L’hypothèse de l’augmentation de l’humidité relative de l’air avec l’altitude a déjà été émise pour cette zone (Gautier et al. 2006), par l’observation d’une densité croissante de végétation nécessitant une importante humidité atmosphérique, comme les forêts recouvertes de mousses et de

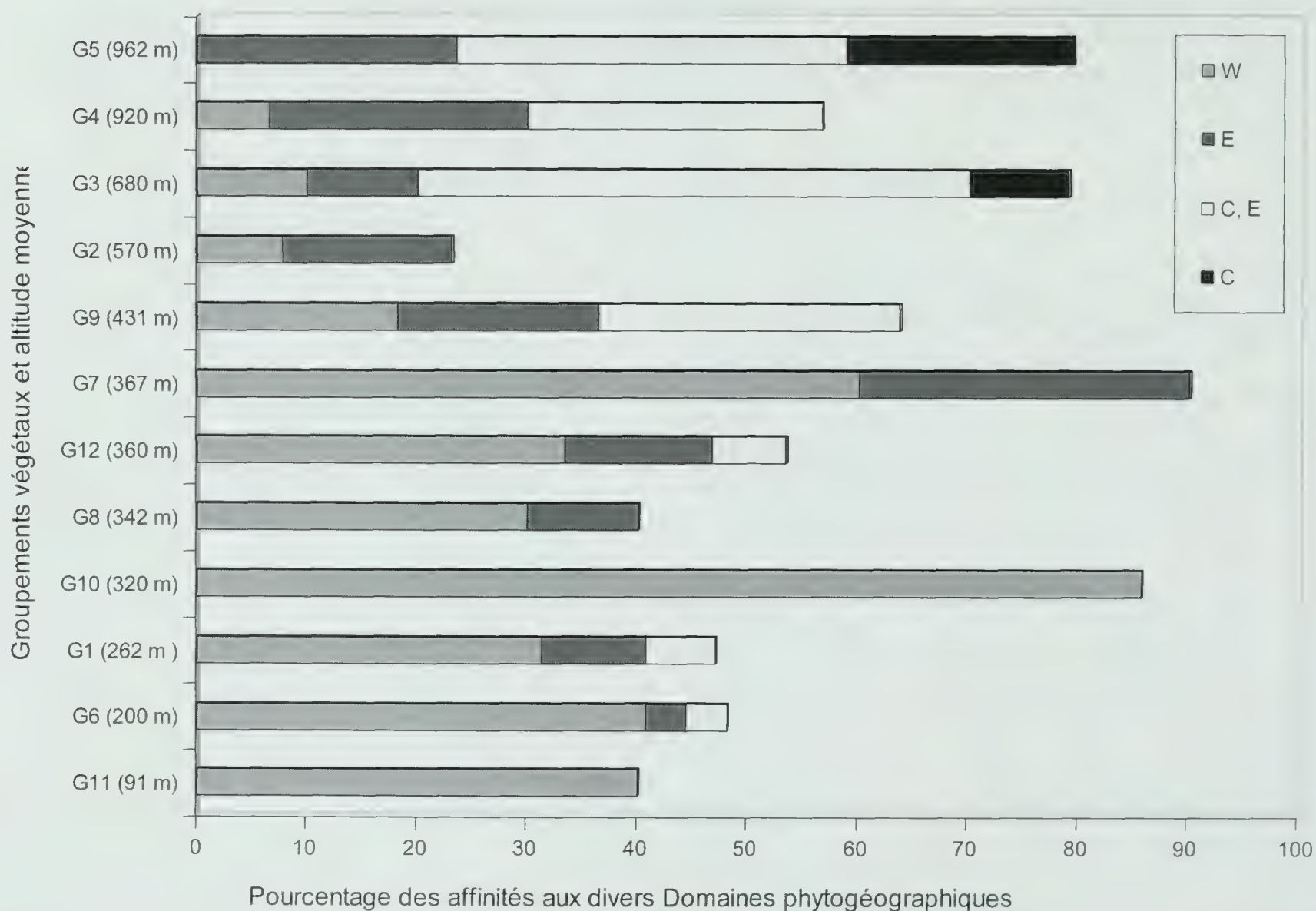


Figure 1 Histogramme cumulé des pourcentages des affinités aux Domaines phytogéographiques des espèces indicatrices des groupements végétaux. En abscisse les pourcentages des affinités aux Domaines phytogéographiques des espèces indicatrices de chaque groupement; en ordonnée les groupements végétaux disposés en fonction de l'altitude, groupement en basse altitude vers la base de l'axe et groupement d'altitude vers le haut de l'axe. La moyenne des altitudes des relevés de ces groupements est indiquée entre parenthèse. W: Domaine de l'Ouest, représenté en gris clair; E: Domaine de l'Est, représenté en gris foncé; C, E: espèces à distribution partagée entre domaine de l'Est et du Centre, représenté en blanc; C: Domaine du Centre, représenté en noir.

lichens, à partir d'une certaine élévation. L'importance de l'altitude sur la distribution spatiale des espèces et des types forestiers a également été démontrée pour la zone (Nusbaumer et al. 2010, Ranirison et al. 2010, Ranirison 2010). Nous démontrons ici que cette succession altitudinale des espèces caractéristique des groupements végétaux va de pair avec une structuration phytogéographique. Les basses altitudes, plus sèches, permettent l'installation de types forestiers affins à ceux rencontrés dans le Domaine de l'Ouest mais ne permettent pas celle des types forestiers nécessitant plus d'humidité (Domaine de l'Est, Centre, Sambirano). Les zones situées en altitude, plus humides et plus fraîches sont favorables à l'installation des types forestiers affins de ceux rencontrés dans le Domaines de l'Est et/ou du Centre. Sur les sommets, les conditions climatiques plus extrêmes (vent, insolation, température) limitent le développement des types forestiers affins du Domaine de l'Est et ne laissent s'installer que les types forestiers affins au Domaine du Centre. Nusbaumer (2011) arrive à des conclusions similaires en se basant de l'étude de la distribution des espèces les plus fréquentes.

Les limites altitudinales de ces 'unités floristiques' concordent à quelques différences près avec celles établies pour l'ensemble du territoire malgache par Humbert (1951, 1955) et par Humbert & Cours Darne (1965). Sur la carte des Domaines Phytogéographique de Madagascar (Humbert 1955) l'attribution de l'ensemble de la région Loky-Manambato au Domaine de l'Ouest est due au manque de connaissance de cette région lors de la réalisation de la carte et au fait que la carte de l'ensemble de l'île ne peut considérer un niveau de détail si élevé.

La coexistence sur une surface restreinte des types forestiers affins au Domaine de l'Ouest, de l'Est, du Centre et du Sambirano confirme la complexité de la zone Loky-Manambato. La présence des types forestiers affins au Domaine de l'Ouest en basse altitude se fond dans le paysage global actuel du nord de Madagascar qui est inclus dans ce Domaine. L'existence des types forestiers affins aux Domaines de l'Est et du Centre est une particularité rare dans les régions alentours. La zone Loky-Manambato aurait été jadis couverte de forêts plus humides en continuité avec les domaines du centre et de l'Est pendant le dernier épisode interglaciaire pluviale (Goodman & Wilmé 2006). L'état actuel des formations

végétales serait le résultat d'un assèchement du climat d'une manière générale (Burney 1996, Straka 1996, Burney 1997). La répartition spatiale des types forestiers humides, qui sont réfugiés dans des endroits présentant encore des conditions climatiques favorables à travers les divers îlots forestiers (haut de versant et sommets en altitude), met en évidence les caractères relictuels de ces formations végétales.

CONCLUSION

La région Loky-Manambato est une zone d'un grand intérêt au niveau de la variabilité des groupements végétaux qui composent ses forêts. Sa situation géographique dans le nord-est de Madagascar, limité par l'Océan Indien à l'Est et la présence de quelques massifs culminant à plus de 1000 m, lui confère une diversité de paramètres écologiques, qui ont une forte influence sur la distribution des groupements végétaux.

La classification d'unités de végétation en groupements végétaux permet non seulement de comprendre les facteurs qui régissent la distribution de la végétation mais un tel classement permet également de replacer une zone dans un contexte phytogéographique à plus large échelle. La répartition spatiale des unités phytogéographiques de la Loky-Manambato est influencée par l'altitude mais leur succession dépend également de la paléohistoire de la zone.

Les types forestiers présentant des affinités avec les Domaines de végétation humides se rencontrent généralement en moyenne et haute altitude. Inversement, ceux qui possèdent des affinités avec les Domaines de végétation secs se rencontrent souvent en basse altitude. Les forêts de transition qui présentent des affinités mixtes entre les phytochories sèches et humides se retrouvent à des altitudes intermédiaires dans cette zone, c'est-à-dire entre 200 et 600 m d'altitude.

Les différentes méthodes d'études adoptées dans ce travail sont fiables et permettent l'obtention de résultats assez pointus pour étudier une zone de transition comme le cas de la Loky-Manambato. La présente recherche contribue à la connaissance botanique de cette zone dont certaines branches comme la paléobotanique méritent une attention particulière pour les recherches à entreprendre.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible au format pdf sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> - SBB50 > dossier 589) et consiste en une liste floristique des espèces indicatrices par groupe.

REMERCIEMENTS

Nous tenons à remercier toutes les personnes et les institutions partenaires et bailleurs qui nous ont permis de mener à bien nos recherches: la Direction Générale de l'Environnement et des Forêts de Madagascar (DGEF), Conservation International (CI), l'ONG Fanamby, les Conservatoire et Jardin botaniques de la Ville de Genève (CJBG), les Universités d'Antananarivo et de Genève (UNIGE) ainsi

que la Vontobel Stiftung. Le premier auteur tient à remercier la Commission fédérale des bourses pour étudiants étrangers (CFBE) de la Confédération Helvétique. L'intervention du premier auteur lors XIX Congrès de l'AETFAT a été soutenue par l'Initiative Sud Expert Plantes.

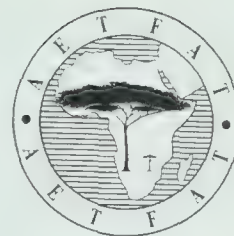
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Manuscript received 31 Oct. 2010; accepted in revised version 9 May 2012.

Communicating Editor: Porter P. Lowry II.



Checklist of the aloes of Madagascar and the Western Indian Ocean Islands: towards an interactive identification mechanism

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Background – The genus *Aloe* L. is distributed on Africa (with the majority of species), the Arabian Peninsula, Socotra, Madagascar and the Mascarene Islands. The berried aloes, previously separated in the genus *Lomatophyllum* Willd., are included as a section of the genus *Aloe*.

Aim – The Madagascan component of the Aloes of the World project, a part of the African Plants Initiative, has been prioritised and an electronic interactive key to the aloes of Madagascar and the Western Indian Ocean Islands are being produced.

Results and discussion – Madagascar is home to ± 151 taxa which are all endemic, while Rodrigues and Reunion each harbour one species, Mauritius two species, Aldabra one and the Comores two. The aloes of the small islands are all berried aloes. New species are constantly being discovered and the taxonomy of the genus on the Red Island is improving as more fieldwork expands our knowledge of the aloes of this biodiversity hotspot.

Key words – *Aloe*, *Lomatophyllum*, Asphodelaceae / Aloaceae, Madagascar, Western Indian Ocean Islands, identification key, checklist, Lucid software.

ALOES OF THE WORLD PROJECT

The genus *Aloe* L. is distributed in Africa (with the majority of species), the Arabian Peninsula, Socotra, Madagascar and the Mascarene Islands. The Aloes of the World project, a part of the African Plants Initiative, aims to provide a comprehensive electronic facility that pulls together all relevant information and available images in a web-based, user-friendly information bank.

MADAGASCAN COMPONENT

The Madagascan component of the Aloes of the World project has been prioritised and an electronic interactive key to the aloes of Madagascar and the Western Indian Ocean Islands (fig. 1) is currently being produced. Once the electronic interactive key is finalised, it will be made available on the Lucid website (<http://www.lucidcentral.org>).

Madagascar is home to ± 151 taxa which are all endemic, while Rodrigues and Réunion each harbour one endemic species, Mauritius two endemic species, Aldabra one endemic and the Comores two endemic species. There are no aloes known from the Seychelles Islands. The aloes of the small islands are all berried aloes, previously segregated in the genus *Lomatophyllum* Willd., which are now included as a section of the genus *Aloe*.

METHODOLOGY

Descriptions

Comprehensive descriptions based on the Aloes of the World template for all taxa were compiled using various literature sources, including:

- *Les Lomatophyllum et les Aloe de Madagascar* (Perrier de la Bâthie 1926)
- *Flore de Madagascar* (Perrier de la Bâthie 1938a, 1938b)

- *The aloes of tropical Africa and Madagascar* (Reynolds 1966)
- *Flore des Mascareignes, la Réunion, Maurice, Rodrigues* (Marais 1978a, 1978b)
- *Succulent and xerophytic plants of Madagascar* (Rauh 1995, 1998a)
- *Illustrated handbook of succulent plants: Monocotyledons* (Newton 2001)
- *Les aloe de Madagascar / The aloe of Madagascar* (Castillon & Castillon 2010)
- and the protologues for the taxa (protologue dates of current taxa and their basionyms are indicated in the checklist and full literature citations appear in the reference list).

Draft descriptions and additional information were sent to experts to check and amend.

Lucid Software

The electronic interactive key is being produced using Lucid, a software package developed by the Centre for Biological Information Technology (CBIT) at the University of Queensland, Australia. Lucid software represents powerful and flexible tools specifically designed for identification and diagnostic purposes. It enables the management and accumulation of information in a user-friendly system that can be distributed to a wide audience on CD, DVD or through the internet (<http://www.lucidcentral.org>).

CHECKLIST TO THE ALOES OF MADAGASCAR AND THE WESTERN INDIAN OCEAN ISLANDS

- ^M – Madagascar, endemic
- ^{Re} – Réunion, endemic
- ^{Ro} – Roderigues, endemic
- ^{Ma} – Mauritius, endemic
- [^] – Aldabra, endemic
- ^{CC} – Comoros, endemic
- ^{CM} – Mayotte (Comoros), endemic
- * – naturalised

Aloe L.

- ^M *Aloe acutissima* H.Perrier (1926) var. *acutissima*
- ^M *Aloe acutissima* H.Perrier var. *antanimorensis* Reynolds (1956a)
- ^M *Aloe acutissima* H.Perrier var. *fiherenensis* J.-B.Castillon (2007c)
- ^M *Aloe acutissima* H.Perrier var. *isaloana* J.-B.Castillon (2007c)
- ^M *Aloe acutissima* H.Perrier subsp. *itampolensis* Rebmman (2008a)
- A. acutissima* H.Perrier var. *itampoloana* J.-B.Castillon
- Aloe acutissima* H.Perrier var. *itampoloana* J.-B.Castillon = *A. acutissima* H.Perrier var. *itampolensis* Rebmman
- ^M *Aloe albiflora* Guillaumin (1940)
- Guillauminia albiflora* (Guillaumin) A.Bertrand

- ^M *Aloe albostriata* T.A.McCoy, Rakouth & Lavranos (2008)
- ^A *Aloe aldabrensis* (Marais) L.E.Newton & G.D.Rowley (Rowley 1996)
- Lomatophyllum aldabrense* Marais (1974)
- Lomatophyllum borbonicum* Baker
- ^{CC} *Aloe alexandrei* Ellert (2006)
- ^M *Aloe alfredii* Rauh (1990)
- Aloe altimatsiatrae* J.-B.Castillon = *A. fievetii* Reynolds var. *altimatsiatrae* (J.-B.Castillon) J.-B.Castillon
- ^M *Aloe ambositrae* J.-P.Castillon (2008a)
- ^M *Aloe ambrensis* J.-B.Castillon (2007a)
- ^M *Aloe ampefyana* J.-B.Castillon (2007b)
- Aloe andohahelensis* J.-B.Castillon = *A. teissieri* Lavranos
- ^M *Aloe andringitrensis* H.Perrier (1926)
- ^M *Aloe anivoranoensis* (Rauh & Hebding) L.E.Newton & G.D.Rowley (Rowley 1996)
- Lomatophyllum anivoranoense* Rauh & Hebding (Rauh 1998b)
- ^M *Aloe ankaranensis* Rauh & Mangelsdorff (2000b)
- ^M *Aloe* × *anosyana* J.-P.Castillon (2012a) [natural hybrid, *A. divaricata* A.Berger subsp. *vaotsohy* (Decorse & Poiss.) J.-P.Castillon × *A. helenae* Danguy]
- ^M *Aloe antandroi* (Decary) H.Perrier (1926) subsp. *antandroi*
- A. leptocaulon* Bojer (nom.nud.)
- Gasteria antandroi* Decary (1921)
- ^M *Aloe antandroi* (Decary) H.Perrier subsp. *toliarana* J.-B.Castillon (2009b)
- ^M *Aloe antonii* J.-B.Castillon (2006a)



Figure 1 – Map of the area covered by the interactive key to the aloes of Madagascar and the Western Indian Ocean Islands.

^M *Aloe antsingyensis* (Leandri) L.E.Newton & G.D.Rowley (Rowley 1996)
Lomatophyllum antsingyense Leandri (1935)

^M *Aloe argyrostachys* Lavranos, Rakouth & T.A.McCoy (2007)

^M *Aloe aurelienii* J.-B.Castillon (2008c)

^M *Aloe bakeri* Scott-Elliot (1891)
Guillauminia bakeri (Scott-Elliot) P.V.Heath
Aloe barbadensis Mill. = *A. vera* (L.) Burm.f.

^M *Aloe belavenokensis* (Rauh & Gerold) L.E.Newton & G.D.Rowley (Rowley 1996)
Lomatophyllum belavenokense Rauh & Gerold (Rauh 1993)

^M *Aloe bellatula* Reynolds (1956b) [probably conspecific with *A. perrieri* Reynolds]
Guillauminia bellatula (Reynolds) P.V.Heath

^M *Aloe berevoana* Lavranos (1998)

^M *Aloe bernadettae* J.-B.Castillon (2000)

^M *Aloe betsileensis* H.Perrier (1926)

^M *Aloe boiteaui* Guillaumin (1942)
Leemea boiteaui (Guillaumin) P.V.Heath

^M *Aloe bosseri* J.-B.Castillon (2000)

^M *Aloe bruynsii* P.I.Forst. (2003)

^M *Aloe buchlohii* Rauh (1966)

^M *Aloe bulbillifera* H.Perrier (1926) var. *bulbillifera*

^M *Aloe bulbillifera* H.Perrier var. *paulianae* Reynolds (1956a)

^M *Aloe calcairophila* Reynolds (1961)
Guillauminia calcairophila (Reynolds) P.V.Heath

^M *Aloe capitata* Baker var. *angavoana* J.-P.Castillon (2009b)

^M *Aloe capitata* Baker (1883) var. *capitata*
A. cernua Tod.

Aloe capitata Baker var. *cipolinicola* H.Perrier = *A. cipolinicola* (H.Perrier) J.-B.Castillon & J.-P.Castillon

Aloe capitata Baker var. *gneissicola* H.Perrier = *A. gneissicola* (H.Perrier) J.-B.Castillon & J.-P.Castillon

^M *Aloe capitata* Baker var. *quartziticola* H.Perrier (1926)

^M *Aloe capitata* Baker var. *silvicola* H.Perrier (1926)

Aloe capitata Baker var. *trachyticola* H.Perrier = *A. trachyticola* (H.Perrier) Reynolds var. *trachyticola*

Aloe capmanambatoensis Rauh & Gerold = *A. fragilis* Lavranos & Rösli

^M *Aloe castilloniae* J.-B.Castillon (2006b)

Aloe cernua Tod. = *A. capitata* Baker var. *capitata*

^M *Aloe charlotteae* J.-B.Castillon (2006d)

^M *Aloe cipolinicola* (H.Perrier) J.-B.Castillon & J.-P.Castillon (2010)
A. capitata Baker var. *cipolinicola* H.Perrier (1926)

^M *Aloe citrea* (Guillaumin) L.E.Newton & G.D.Rowley (Rowley 1996)
Lomatophyllum citreum Guillaumin (1944)

^M *Aloe compressa* H.Perrier (1926) var. *compressa*

^M *Aloe compressa* H.Perrier var. *paucituberculata* Lavranos (1998)

Aloe compressa H.Perrier var. *rugosquamosa* H.Perrier = *A. rugosquamosa* (H.Perrier) J.-B.Castillon & J.-P.Castillon

^M *Aloe compressa* H.Perrier var. *schistophila* H.Perrier (1926)

^M *Aloe conifera* H.Perrier (1926)

Aloe contigua (H.Perrier) Reynolds = *A. imalotensis* Reynolds var. *imalotensis*

Aloe cremersii Lavranos = *A. ibitiensis* H.Perrier, non sensu Reynolds

^M *Aloe cryptoflora* Reynolds (1965)

Aloe cyrillei J.-B.Castillon = *A. ibitiensis* H.Perrier, non sensu Reynolds

^M *Aloe cyrtophylla* Lavranos (1998)

^M *Aloe darainensis* J.-P.Castillon (2009a)

^M *Aloe decaryi* Guillaumin (Guillaumin & Humbert 1941) [probably a robust form of *A. antandroi* (Decary) H.Perrier]

^M *Aloe decorsei* H.Perrier (1926)

^M *Aloe deinacantha* T.A.McCoy, Rakouth & Lavranos (2008) [probably conspecific with *Aloe divaricata* A.Berger subsp. *divaricata*]

^M *Aloe delphinensis* Rauh (1990)

^M *Aloe deltoideodonta* Baker subsp. *amboahangyensis* Rebmman (2009)

^M *Aloe deltoideodonta* Baker var. *brevifolia* H.Perrier (1926)

^M *Aloe deltoideodonta* Baker var. *candicans* H.Perrier (1926)

Aloe deltoideodonta Baker var. *contigua* H.Perrier = *A. imalotensis* Reynolds var. *imalotensis*

Aloe deltoideodonta Baker var. *contigua* H.Perrier f. *latifolia* H.Perrier = *A. imalotensis* Reynolds var. *imalotensis*

Aloe deltoideodonta Baker var. *contigua* H.Perrier f. *longifolia* H.Perrier = *A. imalotensis* Reynolds var. *imalotensis*

Aloe deltoideodonta Baker var. *contigua* H.Perrier f. *variegata* Boiteau = *A. imalotensis* Reynolds var. *imalotensis*

^M *Aloe deltoideodonta* Baker (1883) var. *deltoideodonta* [non Francois (1937)]
A. rossi Tod.

Aloe deltoideodonta Baker subsp. *esomonyensis* Rebmman = *A. deltoideodonta* Baker var. *ruffingiana* (Rauh & Petignat) J.-B.Castillon & J.-P.Castillon

^M *Aloe deltoideodonta* Baker var. *fallax* J.-B.Castillon (2006c)

^M *Aloe deltoideodonta* Baker var. *intermedia* H.Perrier (1926)

^M *Aloe deltoideodonta* Baker var. *ruffingiana* (Rauh & Petignat) J.-B.Castillon & J.-P.Castillon (2010)
A. deltoideodonta Baker subsp. *esomonyensis* Rebmman
A. ruffingiana Rauh & Petignat (1999)

- ^M *Aloe descoingsii* Reynolds subsp. *augustina* Lavranos (1995)
- ^M *Aloe descoingsii* Reynolds (1958) subsp. *descoingsii* Guillauminia *descoingsii* (Lavranos) P.V.Heath
- ^M *Aloe divaricata* A.Berger (1905) subsp. *divaricata*
A. divaricata A.Berger var. *rosea* (Decary) Reynolds
A. sahundra Bojer (nom.nud.)
A. vahontsohy H.Perrier (nom.nud.)
A. vaotsohy Decorse & Poiss. var. *rosea* Decary
- ^M *Aloe divaricata* A.Berger subsp. *vaotsohy* (Decorse & Poiss.) J.-P.Castillon (2012a)
A. vaotsohy Decorse & Poiss. (Poisson 1912), ‘vaotsohy’ & ‘vaotsoy’ Decorse in Notes, Reconn. Explor. 623 (1900) cum fig. without status
- ^M *Aloe divaricata* A.Berger subsp. *tulearensis* (T.A.McCoy & Lavranos) J.-P.Castillon (2012a)
A. tulearensis T.A.McCoy & Lavranos (2007a)
- Aloe divaricata* A.Berger var. *rosea* (Decary) Reynolds = *Aloe divaricata* A.Berger subsp. *divaricata*
- ^M *Aloe droseroides* Lavranos & T.A.McCoy (2003)
- ^M *Aloe edouardii* Rebmman (2008b)
A. fianarantsoae J.-B.Castillon (nom.inval.)
- ^M *Aloe ericetorum* Bosser (1968)
- ^M *Aloe erythrophylla* Bosser (1968)
Aloe estevei Rebmman = *A. fievetii* Reynolds var. *altimatsiatrae* (J.-B.Castillon) J.-B.Castillon
- ^M *Aloe eximia* Lavranos & T.A.McCoy (2006)
Aloe fianarantsoae J.-B.Castillon (nom.inval.) = *A. edouardii* Rebmman
- ^M *Aloe fievetii* Reynolds (1965) var. *fievetii*
- ^M *Aloe fievetii* Reynolds var. *altimatsiatrae* (J.-B.Castillon) J.-B.Castillon (2009b)
A. altimatsiatrae J.-B.Castillon (2008b)
A. estevei Rebmman
- ^M *Aloe fleuretteana* Rauh & Gerold (2000)
- ^M *Aloe florenceae* Lavranos & T.A.McCoy (2004)
Aoe fontainei Rebmman = *A. mandotoensis* J.-B.Castillon
- ^M *Aloe fragilis* Lavranos & Rösli (1994)
A. capmanambatoensis Rauh & Gerold
A. guillaumettii auct., Lavranos & Rösli, Cact. Succ.J.(US) 66: 3–6 (1994) (misapplied name)
- ^M *Aloe gneissicola* (H.Perrier) J.-B.Castillon & J.-P.Castillon (2010)
A. capitata Baker var. *gneissicola* H.Perrier (1926)
- ^M *Aloe guillaumettii* Cremers (1976)
Aloe guillaumettii auct., Lavranos & Rösli, Cact. Succ.J.(US) 66: 3–6 (1994) (misapplied name) = *A. fragilis* Lavranos & Rösli
- ^M *Aloe haworthioides* Baker var. *aurantiaca* H.Perrier (1926) [probably not a good variety]
- ^M *Aloe haworthioides* Baker (1887) var. *haworthioides* [non Francois (1937)]
Aloinella haworthioides (Baker) Lemée (nom. inval.)
Leemea haworthioides (Baker) P.V.Heath
- ^M *Aloe helenae* Danguy (1929)
- ^M *Aloe hoffmannii* Lavranos (2002b)
- ^M *Aloe humbertii* H.Perrier (1931)
- ^M *Aloe ibitiensis* H.Perrier (1926), non sensu Reynolds (1966)
A. cremersii Lavranos
A. cyrillei J.-B.Castillon
A. itremensis Reynolds
A. saronarae Lavranos & T.A.McCoy
- ^M *Aloe ifanadianae* J.-B.Castillon (2008d)
- ^M *Aloe imalotensis* Reynolds (1957) var. *imalotensis*
A. contigua (H.Perrier) Reynolds
A. deltoideodonta Baker var. *contigua* H.Perrier
A. deltoideodonta Baker var. *contigua* H.Perrier f. *latifolia* H.Perrier
A. deltoideodonta Baker var. *contigua* H.Perrier f. *longifolia* H.Perrier
A. deltoideodonta Baker var. *contigua* H.Perrier f. *variegata* Boiteau
- ^M *Aloe imalotensis* Reynolds var. *longeracemosa* J.-B.Castillon (2005)
- ^M *Aloe* × *imerinensis* J.Bosser (1968) [*A. capitata* Baker var. *capitata* × *A. macroclada* Baker]
- ^M *Aloe inexpectata* Lavranos & T.A.McCoy (2003)
Aloe intermedia (H.Perrier) Reynolds, non Haw. (nom. illegit.) = *A. newtonii* J.-B.Castillon
- ^M *Aloe isaloensis* H.Perrier (1927)
Aloe itremensis Reynolds = *A. ibitiensis* H.Perrier, non sensu Reynolds
- ^M *Aloe johannis* J.-B.Castillon (2006c)
- ^M *Aloe johannis-bernardii* J.-P.Castillon (2008b)
- ^M *Aloe johannis-philippeii* J.-B.Castillon (2009a)
- ^M *Aloe laeta* A.Berger (1908) var. *laeta*
- ^M *Aloe laeta* A.Berger var. *maniaensis* H.Perrier (1926) [sometimes considered as a doubtful taxon]
- ^M *Aloe leandrii* Bosser (1968)
Aloe leptocaulon Bojer (nom.nud.) = *A. antandroi* (Decary) H.Perrier
- ^{Re} *Aloe lomatophylloides* Balf.f. (1877) [cultivated on Mauritius]
Lomatophyllum lomatophylloides (Balf.f) Marais
- ^M *Aloe lucile-allorgeae* Rauh (1998b)
- ^{Re} *Aloe macra* Haw. (1819)
Lomatophyllum borbonicum auct., non Willd., sensu Cordem. (1895)
Lomatophyllum macrum (Haw.) Salm-Dyck ex Roem. & Schult.
Phylloma macrum (Haw.) Sweet
- ^M *Aloe macroclada* Baker (1883)
- ^M *Aloe madecassa* H.Perrier var. *lutea* Guillaumin (Guillaumin & Rose 1955) (status doubtful)
- ^M *Aloe madecassa* H.Perrier (1926) var. *madecassa* [non Francois (1937)]

- ^M *Aloe makayana* Lavranos, Rakouth & T.A.McCoy (2008) [sometimes considered a synonym of *A. imalotensis* Reynolds]
- ^M *Aloe manandonae* J.-B.Castillon & J.-P.Castillon (2008)
- ^M *Aloe mandotoensis* J.-B.Castillon (2003)
A. fontainei Rebmann
- ^M *Aloe mandrarensis* J.-P.Castillon (2012b)
Aloe marginalis DC. (nom. superfl.) = *A. purpurea* Lam.
Aloe marginata (Aiton) Willd. = *A. purpurea* Lam.
- ^M *Aloe massawana* Reynolds subsp. *sakoankenke* (J.-B. Castillon) J.-B.Castillon (2009b)
A. sakoankenke J.-B.Castillon (2004b)
- ^{CM} *Aloe mayottensis* A.Berger (1908)
- ^M *Aloe megalocarpa* Lavranos (1998)
- ^M *Aloe millotii* Reynolds (1956a)
- ^M *Aloe mitsioana* J.-B.Castillon (2006d)
- ^M *Aloe namorokaensis* (Rauh) L.E.Newton & G.D.Rowley (Rowley 1996)
Lomatophyllum namorokaense Rauh (1998b)
- ^M *Aloe newtonii* J.-B.Castillon (2009c)
A. intermedia (H.Perrier) Reynolds, non Haw. (nom. illegit.)
A. subacutissima G.D.Rowley (misapplied name)
- ^M *Aloe occidentalis* (H.Perrier) L.E.Newton & G.D.Rowley (Rowley 1996)
Lomatophyllum occidentale H.Perrier (1926)
- ^M *Aloe oligophylla* Baker (1883)
Lomatophyllum oligophyllum (Baker) H.Perrier
- ^M *Aloe orientalis* (H.Perrier) L.E.Newton & G.D.Rowley (Rowley 1996)
Lomatophyllum orientale H.Perrier (1926)
- ^M *Aloe pachydactylos* T.A.McCoy & Lavranos (2007a)
- ^M *Aloe parallelifolia* H.Perrier (1926)
- ^M *Aloe parvula* A.Berger (1908) [non H.Perrier (1926)]
A. sempervivoides H.Perrier
Leemea parvula (A.Berger) P.V.Heath
Aloe parvula auct., sensu H.Perrier (1926 & 1938b), non A.Berger (1908) = *A. perrieri* Reynolds
- ^M *Aloe perrieri* Reynolds (1956b) [probably conspecific with *A. bellatula* Reynolds]
A. parvula auct., sensu H.Perrier (1926 & 1938b), non A.Berger (1908)
- ^M *Aloe peyrierasii* Cremers (1976)
Lomatophyllum peyrierassii (Cremers) Rauh
- ^M *Aloe* ×*philippeii* J.-B.Castillon (2005) [natural hybrid, *A. acutissima* H.Perrier var. *fiherenensis* J.-B.Castillon × *A. viguieri* H.Perrier]
- ^M *Aloe pronkii* Lavranos, Rakouth & T.A.McCoy (2006)
- ^M *Aloe propagulifera* (Rauh & Razaf.) L.E.Newton & G.D.Rowley (Rowley 1996)
Lomatophyllum propaguliferum Rauh & Razaf. (Rauh 1998b)
- ^M *Aloe prostrata* (H.Perrier) L.E.Newton & G.D.Rowley (Rowley 1996)
A. zombitsiensis Rauh & M.Teissier
Lomatophyllum prostratum H.Perrier (1926)
Aloe prostrata (H.Perrier) L.E.Newton & G.D.Rowley subsp. *pallida* Rauh & Mangelsdorff = *A. sakarahensis* Lavranos & M.Teissier subsp. *pallida* (Rauh & Mangelsdorff) Lavranos & M.Teissier
- ^M *Aloe pseudoparvula* J.-B.Castillon (2004a)
- ^{Ma} *Aloe purpurea* Lam. (1783)
A. marginalis DC. (nom. superfl.)
A. marginata (Aiton) Willd.
A. rufocincta Haw.
Dracaena dentata Pers., nom.nov. pro *D. marginata* Ait. (Dracaenaceae)
Dracaena marginata Aiton, non Lam. (nom. superfl.) (Dracaenaceae)
Lomatophyllum aloiflorum (Ker Gawl.) G.Nicholson
Lomatophyllum borbonicum Willd. (nom. superfl.)
Lomatophyllum macrum auct., sensu Baker (1877), quoad plantas Mauritanias tantum
Lomatophyllum marginatum Hoffmanns. (nom. nud.)
Lomatophyllum purpureum (Lam.) T.Durand & Schinz
Lomatophyllum rufocinctum (Haw.) Salm-Dyck ex Roem. & Schult.
Phylloma aloiflorum Ker Gawl. (nom. superfl.)
Phylloma borbonicum (Willd.) Roem. & Schult. (nom. superfl.)
Phylloma rufocinctum (Haw.) Sweet
- ^M *Aloe rapanarivoi* J.-P.Castillon (2009b)
- ^M *Aloe rauhii* Reynolds (1963)
Guillauminia rauhii (Reynolds) P.V.Heath
- ^M *Aloe rebmannii* Lavranos (2002b)
- ^M *Aloe richaudii* Rebmann (2008b)
- ^M *Aloe rodolpheii* J.-B.Castillon (2008a)
- ^M *Aloe roeoeslii* Lavranos & T.A.McCoy (2005)
- ^M *Aloe rosea* (H.Perrier) L.E.Newton & G.D.Rowley (Rowley 1996)
Lomatophyllum roseum H.Perrier (1926)
Aloe rossi Tod. = *A. deltoideodonta* Baker var. *deltoideodonta*
Aloe ruffingiana Rauh & Petignat = *A. deltoideodonta* Baker var. *ruffingiana* (Rauh & Petignat) J.-B.Castillon & J.-P. Castillon
Aloe rufocincta Haw. = *A. purpurea* Lam.
- ^M *Aloe rugosquamosa* (H.Perrier) J.-B.Castillon & J.-P. Castillon (2010)
A. compressa H.Perrier var. *rugosquamosa* H.Perrier (1926)
Aloe sahundra Bojer (nom.nud.) = *A. divaricata* A.Berger subsp. *divaricata*
- ^M *Aloe sakarahensis* Lavranos & M.Teissier subsp. *pallida* (Rauh & Mangelsdorff) Lavranos & M.Teissier (2004)
A. prostrata (H.Perrier) L.E.Newton & G.D.Rowley subsp. *pallida* Rauh & Mangelsdorff (2000a)

^M *Aloe sakarahensis* Lavranos & M.Teissier (2004) subsp. *sakarahensis*
Aloe sakoankenke J.-B.Castillon = *A. massawana* Reynolds subsp. *sakoankenke* (J.-B.Castillon) J.-B.Castillon
Aloe saronarae Lavranos & T.A.McCoy = *A. ibitiensis* H.Perrier, non sensu Reynolds
^M *Aloe schilliana* L.E.Newton & G.D.Rowley (Rowley 1996)
Lomatophyllum viviparum H.Perrier (1926), non *Aloe vivipara* Crantz (1766)
^M *Aloe schomeri* Rauh (1966)
Aloe sempervivoides H.Perrier = *A. parvula* A.Berger
^M *Aloe silicicola* H.Perrier (1926)
^M *Aloe socialis* (H.Perrier) L.E.Newton & G.D.Rowley (Rowley 1996)
Lomatophyllum sociale H.Perrier (1926)
^M *Aloe spinitriaggregata* J.-B.Castillon (2011)
Aloe steffaniana Rauh = *A. versicolor* Guillaumin var. *steffaniana* (Rauh) J.-B.Castillon & J.-P.Castillon
^M *Aloe suarezensis* H.Perrier (1926)
Aloe subacutissima G.D.Rowley (misapplied name) = *A. newtonii* J.-B.Castillon
^M *Aloe suzannae* Decary (1921)
^M *Aloe teissieri* Lavranos (2002a)
A. andohahelensis J.B.Castillon
^{Ma} *Aloe tormentorii* (Marais) L.E.Newton & G.D.Rowley (Rowley 1996)
Lomatophyllum borbonicum auct., non Willd., sensu Baker
Lomatophyllum tormentorii Marais (1974)
^M *Aloe trachyticola* (H.Perrier) Reynolds var. *multifolia* J.-B.Castillon (2004b)
^M *Aloe trachyticola* (H.Perrier) Reynolds (1957) var. *trachyticola*
A. capitata Baker var. *trachyticola* H.Perrier (1926)
Aloe tulearensis T.A.McCoy & Lavranos = *A. divaricata* A.Berger subsp. *tulearensis* (T.A.McCoy & Lavranos) J.-P.Castillon
Aloe vahontsohy H.Perrier (nom.nud.) = *A. divaricata* A.Berger subsp. *divaricata*
^M *Aloe vaombe* Decorse & Poiss. var. *poissonii* Decary (1921) [probably not a good variety]
^M *Aloe vaombe* Decorse & Poiss. (Poisson 1912) var. *vaombe* ['vaombe' Decorse in Notes, Reconn. Explor. 623 (1900), without status]
^M *Aloe vaotsanda* Decary (1921)
Aloe vaotsohy Decorse & Poiss. var. *rosea* Decary = *A. divaricata* A.Berger subsp. *divaricata*
Aloe vaotsohy Decorse & Poiss., 'vaotsohy' & 'vaotsoy' Decorse in Notes, Reconn. Explor. 623 (1900) cum fig., without status = *A. divaricata* A.Berger subsp. *vaotsohy* (Decorse & Poiss.) J.-P.Castillon
^{Ma* Re*} *Aloe vera* (L.) Burm.f. (1768)
A. barbadensis Mill.

^M *Aloe versicolor* Guillaumin (1950) var. *versicolor*
^M *Aloe versicolor* Guillaumin var. *steffaniana* (Rauh) J.-B.Castillon & J.-P.Castillon (2010)
A. steffaniana Rauh (2000)
^M *Aloe viguieri* H.Perrier (1927)
^M *Aloe virginieae* J.-P.Castillon (2012b)
^M *Aloe wernerii* J.-B.Castillon (2007b)
^M *Aloe zakamisyi* T.A.McCoy & Lavranos (2007b)
[sometimes considered a synonym of *A. anivoranoensis* (Rauh & Hebding) L.E.Newton & G.D.Rowley]
Aloe zombitsiensis Rauh & M.Teissier = *A. prostrata* (H.Perrier) L.E.Newton & G.D.Rowley

Aloinella (A.Berger) Lemée

Aloinella haworthioides (Baker) Lemée = *Aloe haworthioides* Baker

Guillauminia A.Bertrand

Guillauminia albiflora (Guillaumin) A.Bertrand = *A. albiflora* Guillaumin
Guillauminia bakeri (Scott-Elliot) P.V.Heath = *A. bakeri* Scott-Elliot
Guillauminia bellatula (Reynolds) P.V.Heath = *A. bellatula* Reynolds
Guillauminia calcairophila (Reynolds) P.V.Heath = *A. calcairophila* Reynolds
Guillauminia descoingsii (Reynolds) P.V.Heath = *A. descoingsii* Reynolds
Guillauminia rauhii (Reynolds) P.V.Heath = *A. rauhii* Reynolds

Lemeea P.V.Heath

Lemeea boiteaui (Guillaumin) P.V.Heath = *A. boiteaui* Guillaumin
Lemeea haworthioides (Baker) P.V.Heath = *A. haworthioides* Baker
Lemeea parvula (A.Berger) P.V.Heath = *A. parvula* A.Berger

Lomatophyllum Willd.

L. aldabrense Marais = *A. aldabrensis* (Marais) L.E.Newton & G.D.Rowley
L. aloiflorum (Ker Gawl.) G.Nicholson = *A. purpurea* Lam.
L. anivoranoense Rauh & Hebding = *A. anivoranoensis* (Rauh & Hebding) L.E.Newton & G.D.Rowley
L. antsingyense Leandri = *A. antsingyensis* (Leandri) L.E.Newton & G.D.Rowley
L. belavenokense Rauh & Gerold = *A. belavenokensis* (Rauh & Gerold) L.E.Newton & G.D.Rowley
L. borbonicum Baker = *A. aldabrensis* (Marais) L.E.Newton & G.D.Rowley

L. borbonicum Willd. (nom.superfl.) = *A. purpurea* Lam.
L. borbonicum auct., non Willd., sensu Baker = *A. tormentorii* (Marais) L.E.Newton & G.D.Rowley
L. borbonicum auct., non Willd., sensu Cordem. (1895) = *A. macra* Haw.
L. citreum Guillaumin = *A. citrea* (Guillaumin) L.E.Newton & G.D.Rowley
L. lomatophylloides (Balf.f) Marais = *A. lomatophylloides* Balf.f.
L. macrum (Haw.) Salm-Dyck ex Roem. & Schult. = *A. macra* Haw.
L. macrum auct., sensu Baker (1877), quoad plantas Mauritanias tantum = *A. purpurea* Lam.
L. marginatum Hoffmanns. (nom.nud.) = *A. purpurea* Lam.
L. namorokaense Rauh = *A. namorokaensis* (Rauh) L.E.Newton & G.D.Rowley
L. occidentale H.Perrier = *A. occidentalis* (H.Perrier) L.E.Newton & G.D.Rowley
L. oligophyllum (Baker) H.Perrier = *A. oligophylla* Baker
L. orientale H.Perrier = *A. orientalis* (H.Perrier) L.E.Newton & G.D.Rowley
L. peyrierassii (Cremers) Rauh = *A. peyrierassii* Cremers
L. propaguliferum Rauh & Razaf. = *A. propagulifera* (Rauh & Razaf.) L.E.Newton & G.D.Rowley
L. prostratum H.Perrier = *A. prostrata* (H.Perrier) L.E.Newton & G.D.Rowley
L. purpureum (Lam.) T.Durand & Schinz = *A. purpurea* Lam.
L. roseum H.Perrier = *A. rosea* (H.Perrier) L.E.Newton & G.D.Rowley
L. rufocinctum (Haw.) Salm-Dyck ex Roem. & Schult. = *A. purpurea* Lam.
L. sociale H.Perrier = *A. socialis* (H.Perrier) L.E.Newton & G.D.Rowley
L. tormentorii Marais = *A. tormentorii* (Marais) L.E.Newton & G.D.Rowley
L. viviparum H.Perrier, non *Aloe vivipara* Crantz (1766) = *A. schilliana* L.E.Newton & G.D.Rowley

Phylloma Ker Gawl.

Phylloma aloiflorum Ker Gawl. = *A. purpurea* Lam.

Phylloma borbonicum (Willd.) Roem. & Schult. = *A. purpurea* Lam.

Phylloma macrum (Haw.) Sweet = *A. macra* Haw.

Phylloma rufocinctum (Haw.) Sweet = *A. purpurea* Lam.

ACKNOWLEDGEMENTS

Prof J.-B. Castillon, Prof J.-P. Castillon and Mr J.J. Lavranos are thanked for their input into the checklist and for checking descriptions of Madagascan and Western Indian Ocean Island aloes; the Lucid production team for technical assistance; Ms L. Ferreira, Interpretation Officer, South African

National Biodiversity Institute, for illustrating the Lucid character list; and two referees for suggesting improvements to the manuscript.

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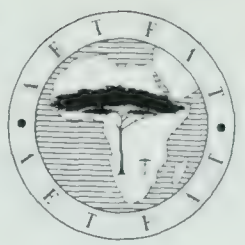
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Manuscript received 27 Oct. 2010; accepted in revised version 14 Jan. 2011.

Communicating Editor: Sylvain Razafimandimbison.



Cyanobactéries et microalgues (Diatomées exclues) du Parc National des Oiseaux du Djoudj (Sénégal)

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Cyanobacteria and microalgae (Diatoms excluded) of the National Ornithological Park of Djoudj (Senegal)

Aims – The present study intends to identify the observed taxa and to determine the structure of the microflora inventoried, in particular the taxonomic and chorologic spectrum.

Methods – The work consisted in making a descriptive study of the morphological characters of the thallus, the colony or the cell of the different taxa and in giving a systematic inventory of the observed taxa. The work was carried out between April 2008 and March 2009 in the National Ornithological Park of Djoudj (PNOD), considered as one of the most important parks for Senegal.

Results – The systematic inventory allowed establishing the structure of the microflora which consists in 74 taxa distributed in 34 genera and twelve families. The taxonomic spectrum indicates that microalgae are dominant and represent 62.2% of the taxa among which 56.8% Chlorophytes and only 5.4% Euglenophytes, followed by Cyanobacteria with 37.8%. Analysis of the chorologic spectrum shows that the microflora of the PNOD is marked by the ascendancy of cosmopolitan and subcosmopolitan taxa representing 71.6% of all observed taxa. Among the 74 taxa, 23 are reported for the first time in Senegal (seven Cyanobacteria, fifteen Chlorophytes and one Euglenophyte).

Key words – Cyanobacteria, Chlorophytes, Euglenophytes, microalgae, taxonomy, identification key, Senegal.

Objectifs – L'étude se propose d'identifier les différents taxons récoltés et de déterminer la structure de la microflore inventoriée, en particulier le spectre taxonomique et le spectre chorologique.

Méthodes – Le travail a consisté en une étude descriptive des caractères morphologiques du thalle, de la colonie ou de la cellule des différents taxons, et en un inventaire systématique des taxons rencontrés. Il a été réalisé entre avril 2008 et mars 2009 dans le Parc National des Oiseaux du Djoudj (PNOD) considéré comme l'un des parcs les plus importants au Sénégal.

Résultats – L'inventaire systématique a permis d'établir la structure de la microflore algale qui est constituée au total de 74 taxons répartis en 34 genres et douze familles. Le spectre taxonomique indique que les microalgues sont dominantes et représentent 62,2% des espèces dont 56,8% de Chlorophytes et seulement 5,4% d'Euglénophytes, suivies des Cyanobactéries avec 37,8% des taxons. L'analyse du spectre chorologique montre que la microflore du PNOD est marquée par la prédominance des espèces cosmopolites et subcosmopolites qui représentent 71,6% des taxons. Parmi les 74 taxons inventoriés, 23 sont rapportés pour la première fois au Sénégal (sept Cyanobactéries, quinze Chlorophytes et un Euglénophyte).

INTRODUCTION

Le Parc National des Oiseaux de Djoudj (PNOD) est considéré comme l'un des parcs les plus importants au Sénégal en raison de sa position géographique, de la richesse de sa

faune ornithologique notamment et de la diversité de ses écosystèmes. Il constitue en effet, avec le Parc de Diawling en Mauritanie, un carrefour de quatre domaines biogéographiques (saharien, tropical sahélien et ceux des zones côtières et marines) composé par un ensemble d'écosystèmes

très diversifiés (cuvettes, marigots, lacs, plaines inondables, terres émergées) favorables à l'accueil et au séjour des oiseaux migrants (Noba et al. 2009).

C'est ainsi qu'il a été inscrit sur la liste des zones humides d'importance internationale de la Convention de Ramsar en 1977 et fait partie, depuis 1981, des biens du Patrimoine Mondial de l'Humanité (Ly et al. 2006).

Au plan de la macroflore, à l'exception des travaux de Noba et al. (2009) qui ont dénombré 132 espèces appartenant à 99 genres et 48 familles, les autres études ont été réalisées au niveau de la vallée du fleuve Sénégal.

Il en est de même pour les microphytes aquatiques (Cyanobactéries et microalgues) qui sont encore peu étudiées au Sénégal malgré un important réseau hydrographique. Parmi les études réalisées, on peut citer celles de Dia & Reynaud (1982), de Compère (1991), de Cogels & Gac (1995), de Carl Bro International (1999), de Berger et al. (2005) et de Ba et al. (2006).

Les diatomées ont fait l'objet de quelques travaux comme ceux de Leuduger-Fortmorel, (1898), de Guermeur (1954), d'Amossé (1970), et de Sow et al. (2005).

Ainsi, la présente étude se propose de contribuer à une meilleure connaissance des microphytes aquatiques du PNOD grâce à une étude descriptive des caractères morphologiques des différents taxons et à un inventaire systématique des Cyanobactéries et des microalgues rencontrées permettant de connaître la composition taxonomique et la richesse spécifique et d'établir le spectre chorologique de ces taxons.

MATERIEL ET METHODE

Présentation du site

Le Parc National des Oiseaux de Djoudj (PNOD) a été créé par décret N° 71 – 471 du 14 avril 1971 afin de sauvegarder un des paysages naturels du delta du fleuve Sénégal, aujourd'hui dominés par la riziculture (Ba et al. 2000). Il constitue actuellement une réserve naturelle couvrant une superficie de 16.000 hectares environ dans le delta du fleuve Sénégal.

Le PNOD (fig.1) est situé à près de 60 km au NE de Saint-Louis entre 16°30' de latitude nord et 16° 10' de longitude ouest (Ba et al. 2000). Il est limité au nord et à l'ouest par le fleuve Sénégal, au sud par le marigot du Gorom (Noba et al. 2009).

La position septentrionale du Djoudj l'intègre dans le domaine sahélien et plus précisément dans le secteur sahélo-saharien (Ba et al. 2000) avec des précipitations faibles et inférieures à 400 mm (Faye 2005). L'humidité relative varie entre 47 et 80% (Kuisseu et al. 2001).

Du point de vue du relief, c'est un milieu très plat (altitude ne dépassant pas 23 m), parsemé de dépressions qui forment des marigots ou des étangs au moment des crues du fleuve Sénégal. La majeure partie de l'eau qui inonde le Parc provient en effet du fleuve: elle y pénètre par les marigots du Djoudj et du Crocodile ainsi que par la rivière Gorom. Il faut cependant noter que ce cycle naturel de crue et de décrue,

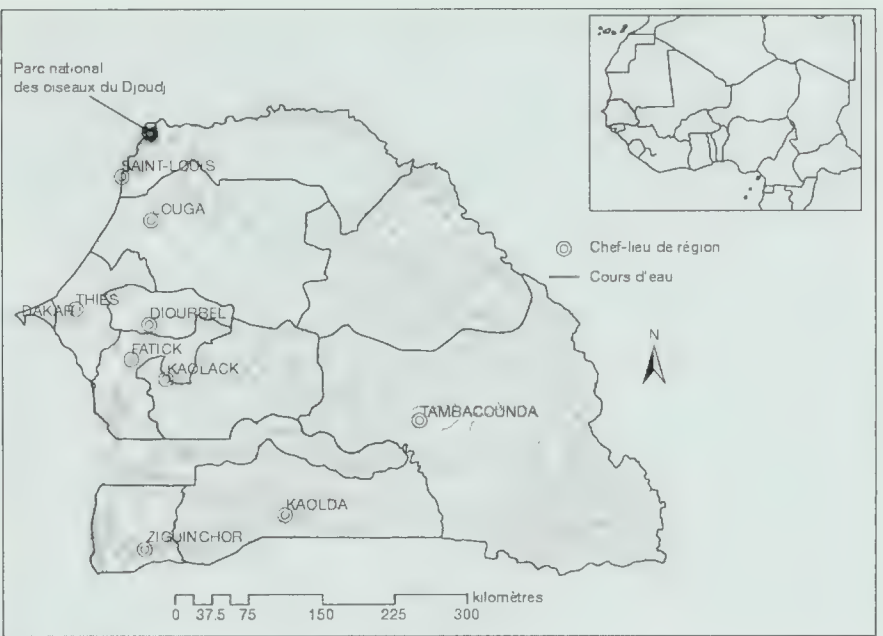


Figure 1 – Localisation du Parc National des Oiseaux du Djoudj (Sénégal).

d'assèchement et de salinité, a été modifié par l'installation du barrage de Diama en service depuis 1986 (Ba et al. 2000).

Méthodologie

Prélèvement – Les Cyanobactéries et microalgues ont été récoltées en avril 2008 et en mars 2009 au niveau des sites mentionnés dans le tableau 1.

Méthodes de récolte et d'échantillonnage – Les récoltes ont été effectuées par prélèvement d'eau (3 litres) à la surface des plans d'eau pour les espèces planctoniques et par grattage de la surface de tout support immergé présent au niveau de la station pour les espèces fixées.

Une partie de l'eau a été recueillie dans des flacons de 60 ml; les échantillons ont été immédiatement fixés in situ avec du formol (4%).

Observation – Les espèces ont été étudiées au microscope photonique à l'objectif à immersion de 100x. Des dessins ont été réalisés ainsi que des mesures de dimensions grâce à un oculaire micrométrique étalonné.

Identification des taxons – A partir de la description, des dessins et des dimensions, l'identification des taxons a été faite par comparaison à certains travaux de base et des pu-

Tableau 1 – Répartition des sites de prélèvement.

Marigots	Sites de prélèvement	Coordonnées UTM	
		X	Y
Djoudj	Djoudj 1	361228	1815102
	Djoudj 2	362202	1816509
	Djoudj 3	362531	1816850
	Nichoir Pélicans 1	364200	1815437
	Nichoir Pélicans 2	364319	1815699
	Gorom 1	363834	1809585
Gorom	Gorom 2	363832	1809350
	Gorom 3	363824	1809299
	Gorom 4	364144	1809102

blications spécialisées comme Bourrelly (1961, 1966, 1968), Bourrelly & Couté (1982, 1986a, 1986b), Compère (1974, 1975, 1976, 1977), Couté & Iltis (1984, 1988), Ferragut et al. (2005), Iltis (1971, 1972), Komárek (2005), Mezenes & Domingos (1994), Phung et al. (1992), Tell & Couté (1993), Thérézien (1986), Berger et al. (2005) et Ba et al. (2006).

Inventaire et richesse spécifique de la microflore – La richesse spécifique de la microflore du PNOD a été déterminée après identification des taxons.

RESULTATS ET DISCUSSION

Morphologie des Cyanobactéries rencontrées

Aphanothece Nägeli – *Aphanothece elabens* (Bréb.) Elenk. (fig. 2A): colonie gélatineuse irrégulière avec des cellules ellipsoïdales pourvues de pseudovacuoles ou aérotopes; diamètre des cellules de 3–4 µm, correspondant à celui donné par Compère (1974).

Merismopedia Meyen – Le genre *Merismopedia* se présente sous forme de colonie tabulaire avec des cellules régulièrement disposées en rangées verticales et horizontales dans une gelée homogène.

Merismopedia tenuissima Lemm. (fig. 2I): cellules subsphériques de 0,5 µm de diamètre. La taille des spécimens observés présente le même ordre de grandeur que ceux décrits par Compère (1974).

Synechocystis Sauv. – Le genre *Synechocystis* présente des cellules sphériques ou subsphériques solitaires mais qui peuvent parfois se regrouper par paire.

Synechocystis aquatilis Sauv. (fig. 2J): cellules sphériques solitaires, parfois groupées par paire; diamètre de 3,5 µm. Les cellules observées présentent le même diamètre que celles décrites par Ferragut et al. (2005).

Synechococcus Nägeli – Le genre *Synechococcus* est aussi caractérisé par des cellules solitaires mais pouvant aussi former de courtes chaînes. Ces cellules sont ovoïdes, ellipsoïdales ou cylindriques.

Avec un diamètre de 3 µm, les cellules de *Synechococcus ambiguus* Skuja (fig. 2K) sont cylindriques, arrondies aux extrémités, solitaires ou parfois groupées par deux. Ces caractères sont également notés par Iltis (1972).

Arthrospira Stit. ex Gom. – Le genre *Arthrospira* est constitué d'un trichome cylindrique hélicoïdal, avec des cloisonnements bien visibles. Il ne présente ni hétérocyte, ni akinète, ni gaine.

Arthrospira platensis var. *non-constricta* (Banerji) Deska-chary (fig. 3C) dispose d'un trichome non rétréci aux articulations et présente de nombreuses granulations. Ses cellules sont rectangulaires. Le diamètre du trichome est de 5 µm et est égal à celui du type rencontré par Berger et al. (2005).

Oscillatoria Vauch. ex Gom. – Le genre *Oscillatoria* est caractérisé par un trichome droit parfois légèrement contourné vers l'extrémité. Le trichome est dépourvu d'hétérocyte, d'akinète et de gaine.

Oscillatoria foreau Frémy (fig. 3F), à trichome droit et rétréci aux articulations, présente des cellules rectangulaires. La longueur des cellules est de 4 µm. Nos échantillons ont

le même ordre de grandeur que ceux décrits par Compère (1974).

Chroococcus Nägeli – Le genre *Chroococcus* est caractérisé par des cellules sphériques ou subsphériques groupées par deux, quatre ou huit, rarement par seize, dans une colonie gélatineuse. En plus, chaque cellule est entourée d'une gaine gélatineuse individuelle.

Les espèces du genre *Chroococcus* rencontrées se distinguent par la forme et la taille des cellules.

Chroococcus minor (Kütz.) Nägeli (fig. 2C) présente une colonie formée de deux cellules sphériques de 4 à 4,5 µm de diamètre et se distingue de *C. minutus* (Kütz.) Nägeli (fig. 2D) et de *C. limneticus* Lemm. (fig. 2B) qui ont des colonies de quatre cellules subsphériques. Le diamètre des cellules est de 6 µm chez *C. minutus* tandis qu'il est de 10 µm chez *C. limneticus*. Les cellules de *C. limneticus* ont le même diamètre (10 µm) que celles de l'espèce mentionnée par Compère (1974).

Le diamètre des cellules de *C. minutus* (6 µm) est supérieur à celui des cellules de l'espèce rencontrée par Ba et al. (2006) qui est de 5 µm et dont la colonie renferme huit cellules.

Les cellules de *C. minor* présentent le même ordre de grandeur que celles observées par Compère (1974).

Microcystis Lemm. – Le genre *Microcystis* forme des colonies gélatineuses sphériques, cylindriques ou irrégulières. Ses cellules peuvent être sphériques ou subsphériques.

La forme des cellules, la présence ou l'absence de pseudovacuoles, la distribution des cellules dans la colonie et leur taille permettent de différencier les taxons du genre *Microcystis*.

Les cellules de *Microcystis delicatissima* (W.West & G.S.West) Starmach (fig. 2F), de diamètre égal à 1 µm, forment une colonie sphérique dans laquelle elles sont distribuées de manière éparse par opposition aux cellules de *M. aeruginosa* (Kütz.) Lemm. (fig. 2E), de *M. incerta* (Lemm.) Lemm. (fig. 2H) et de *M. densa* W.West & G.S.West (fig. 2G) densément regroupées. Les cellules de *M. aeruginosa*, de diamètre compris entre 4 et 5 µm, sont pourvues de pseudovacuoles contrairement aux cellules de *M. densa* et *M. incerta* dont les diamètres respectifs sont de 5 µm et 3 µm.

Les caractères observés chez ces taxons ont été également décrits par Compère (1974).

Anabaena Bory ex Born. & Flah. – Le genre *Anabaena* est caractérisé par des trichomes simples, droits ou diversement enroulés, pourvus d'hétérocystes intercalaires. Ces trichomes peuvent aussi présenter des akinètes.

La forme du trichome et de ses extrémités ainsi que la forme des cellules permettent de différencier les taxons du genre *Anabaena*.

Chez *Anabaena spiroides* Kleb. (fig. 2L) et *Anabaena* sp. (fig. 2O), les cellules végétatives sont sphériques contrairement à celles d'*A. sphaerica* Born. & Flahault (fig. 2M), d'*A. azollae* Strasburger (fig. 2N) et d'*A. sphaerica* f. *temis* G.S.West (fig. 2P). Cependant *A. spiroides* présente un trichome irrégulièrement enroulé avec des akinètes interca-

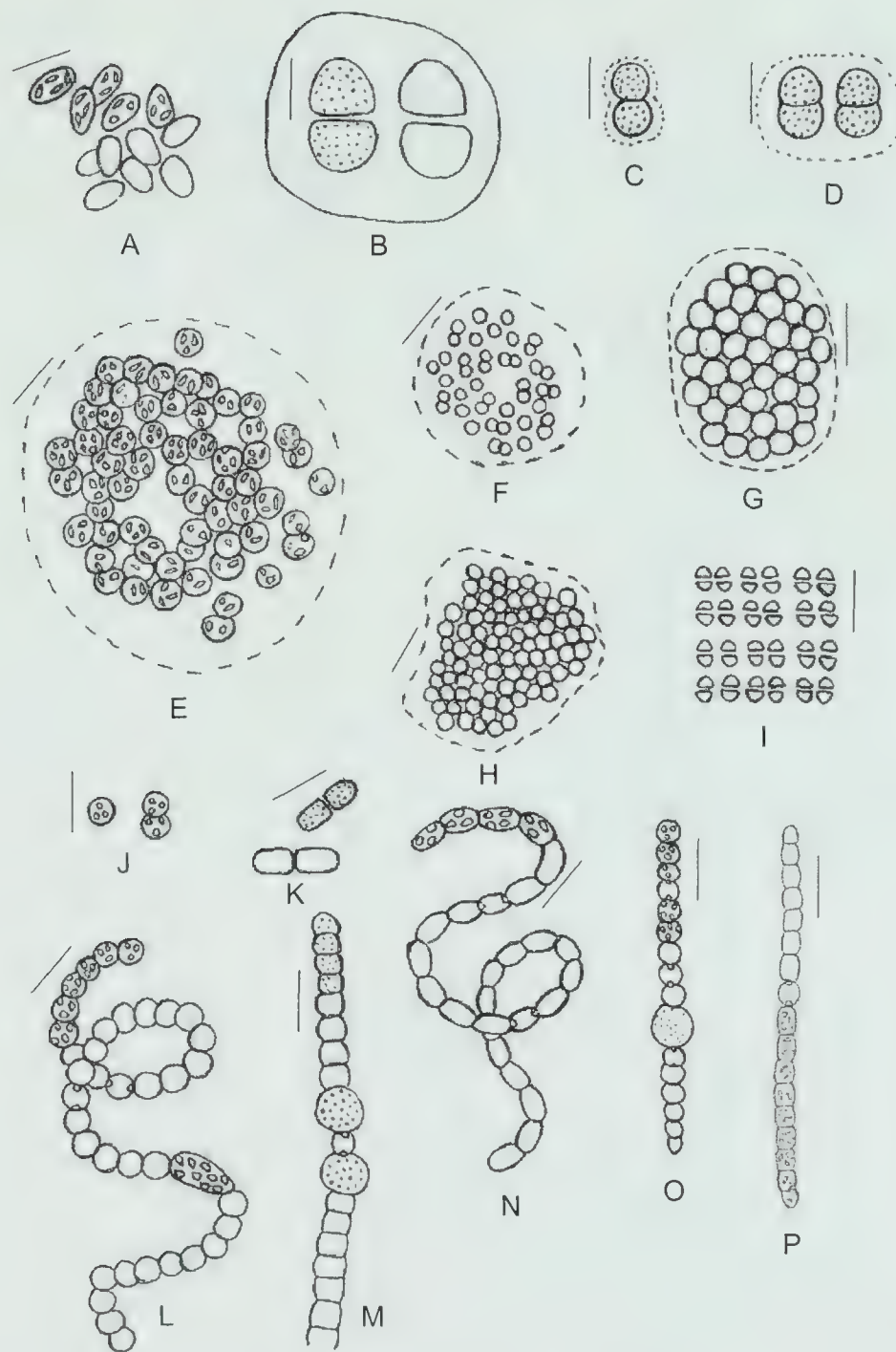


Figure 2 – A, *Aphanothece elabens*; B, *Chroococcus limneticus*; C, *Chroococcus minor*; D, *Chroococcus minutus*; E, *Microcystis aeruginosa*; F, *Microcystis delicatissima*; G, *Microcystis densa*; H, *Microcystis incerta*; I, *Merismopedia tenuissima*; J, *Synechocystis aquatilis*; K, *Synechococcus ambiguus*; L, *Anabaena spiroides*; M, *Anabaena sphaerica*; N, *Anabaena azollae*; O, *Anabaena* sp.; P, *Anabaena sphaerica* f. *tenuis*. Les traits d'échelle représentent chacun 10 µm.

laïres ovoïdes ($17 \times 7 \mu\text{m}$) alors que le trichome chez *Anabaena* sp. est droit avec un apex effilé.

Pour *A. azollae* et *A. sphaerica* var. *tenuis*, les cellules végétatives pourvues de pseudovacuoles sont cylindriques, avec un diamètre respectivement de $6 \mu\text{m}$ et $3\text{--}4 \mu\text{m}$, contrairement à celles d'*Anabaena sphaerica* qui sont subsphériques. Toutefois, les hétérocystes sont courtement cylindriques ($8 \times 6 \mu\text{m}$) chez *A. azollae* à trichome enroulé et sphériques ($3,5 \mu\text{m}$) chez *A. sphaerica* var. *tenuis* dont le trichome est droit et à extrémités effilées.

Comparées aux travaux de Compère (1974), *A. azollae*, *A. sphaerica* et *A. spiroides* présentent les mêmes caractéristiques morphologiques. Par contre la description d'*A. sphaerica* var. *tenuis* correspond bien à celle de Berger et al. (2005).

Raphidiopsis F.E.Fritsch & F.Rich – Le genre *Raphidiopsis* est caractérisé par un trichome à extrémités effilées et à articles cylindriques. Comme le genre *Anabaena*, le genre

Raphidiopsis peut présenter des akinètes mais aucun hétérocyste n'a été observé.

La forme en croissant ou en S de *Raphidiopsis curvata* F.E.Fritsch & M.F.Rich (fig. 3A) permet de la distinguer de *R. mediterranea* Skuja (fig. 3B) qui a un trichome droit. Le diamètre du trichome est de $3 \mu\text{m}$ pour *R. curvata* et de $3,5 \mu\text{m}$ pour *R. mediterranea*. Tous les deux taxons sont pourvus de pseudovacuoles mais seule *R. curvata* présente ici un akinète. L'akinète est subterminal contrairement à l'espèce *R. curvata* décrite par Compère (1974) qui a un akinète en position centrale.

Komvophoron Anagn. & Komárek – Le trichome du genre *Komvophoron* est constitué de cellules apparemment non jointives lié à l'accumulation de vacuoles à gaz au niveau des cloisons et présente deux aérotopes ou pseudovacuoles en forme d'"yeux" à l'apex.

Le nombre et la localisation des pseudovacuoles permettent de distinguer les deux taxons rencontrés.

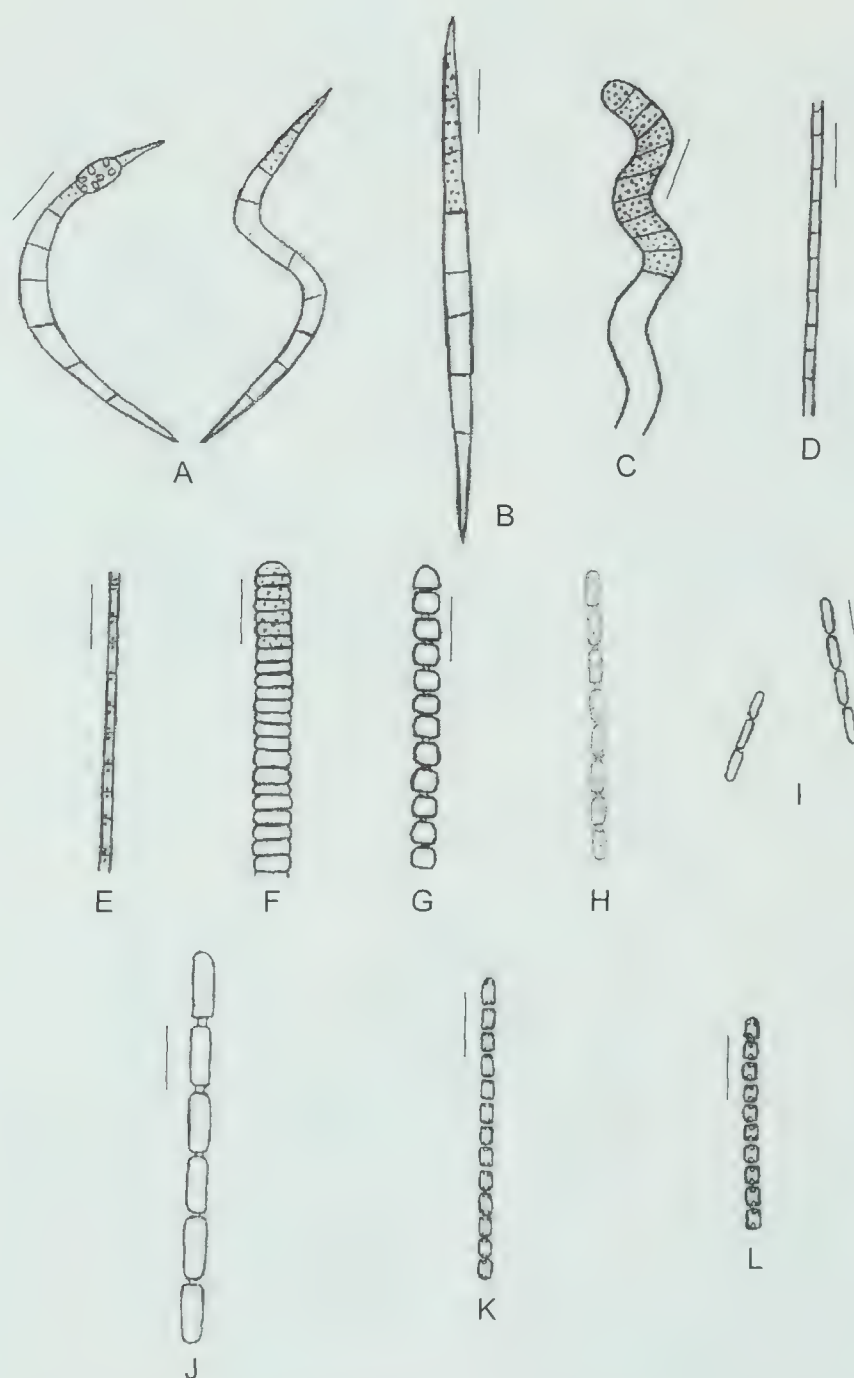


Figure 3 – A, *Raphidiopsis curvata*; B, *Raphidiopsis mediterranea*; C, *Arthrospira platensis* var. *non-constricta*; D, *Lyngbya orientalis*; E, *Lyngbya perelegans*; F, *Oscillatoria foreau*; G, *Pseudanabaena africana*; H, *Pseudanabaena catenata*; I, *Pseudanabaena mucicola*; J, *Pseudanabaena* sp.; K, *Komvophoron minutum*; L, *Komvophoron* sp. Les traits d'échelle représentent chacun 10 µm.

K. minutum (Skuja) Anagn. & Komárek (fig. 3K) et *Komvophoron* sp. (fig. 3L) présente des cellules cylindriques dont les dimensions respectives sont $3 \times 2 \mu\text{m}$ et $3,5 \times 1,5\text{--}2 \mu\text{m}$. Toutefois, *Komvophoron* sp. présente en plus 4 aérotopes au niveau des cloisons.

Pseudanabaena Lauterb. – Le genre *Pseudanabaena* est aussi caractérisé par un trichome à cellules apparemment non jointives mais ne présente pas de pseudovacuoles à l'apex.

Chez les espèces rencontrées, seule *Pseudanabaena africana* G.H.Schwabe (fig. 3G) a des cellules plus ou moins carrées contrairement aux autres taxons dont les cellules sont cylindriques.

Pseudanabaena sp. (fig. 3J) est formée de cellules dont le diamètre est de $3 \mu\text{m}$ contrairement à *P. catenata* Lauterborn (fig. 3H) et *P. mucicola* (Naumann & Huber Pestalozzi) G.H.Schwabe (fig. 3I) qui ont des diamètres inférieurs à $3 \mu\text{m}$. Il est de $2 \mu\text{m}$ chez *P. catenata* et de $1 \mu\text{m}$ chez *P. mucicola* dont le trichome est court et souvent présent dans la gelée de *Microcystis aeruginosa*.

***Lyngbya* s.l.** – Le genre *Lyngbya* C.Agardh est pourvu d'une gaine. Le filament peut être droit, spiralé ou irrégulièrement enroulé. Il ne présente ni hétérocyste, ni akinète.

Cette gaine est étroite chez les deux taxons à filament droit que nous avons récoltés. *Leptolyngbya orientalis* (G.S.West) Anagn. & Komárek (fig. 3D) et *L. perelegans* (Lemmerm.) Anagn. & Komárek (fig. 3E) ont des cellules cylindriques de même diamètre $1,5 \mu\text{m}$. Cependant *L. perelegans* présente des granules réfringents au niveau des cloisons et a le même diamètre que celle décrite par Ba et al. (2006).

Morphologie des Chlorophytes rencontrées

Polyedriopsis Schmidle – Le genre *Polyedriopsis* est caractérisé par des cellules solitaires en coussinets polyédriques à angles prolongés par des soies.

Polyedriopsis spinulosa Schmidle (fig. 4E) présente des cellules à quatre angles arrondies et à côtés concaves; chaque

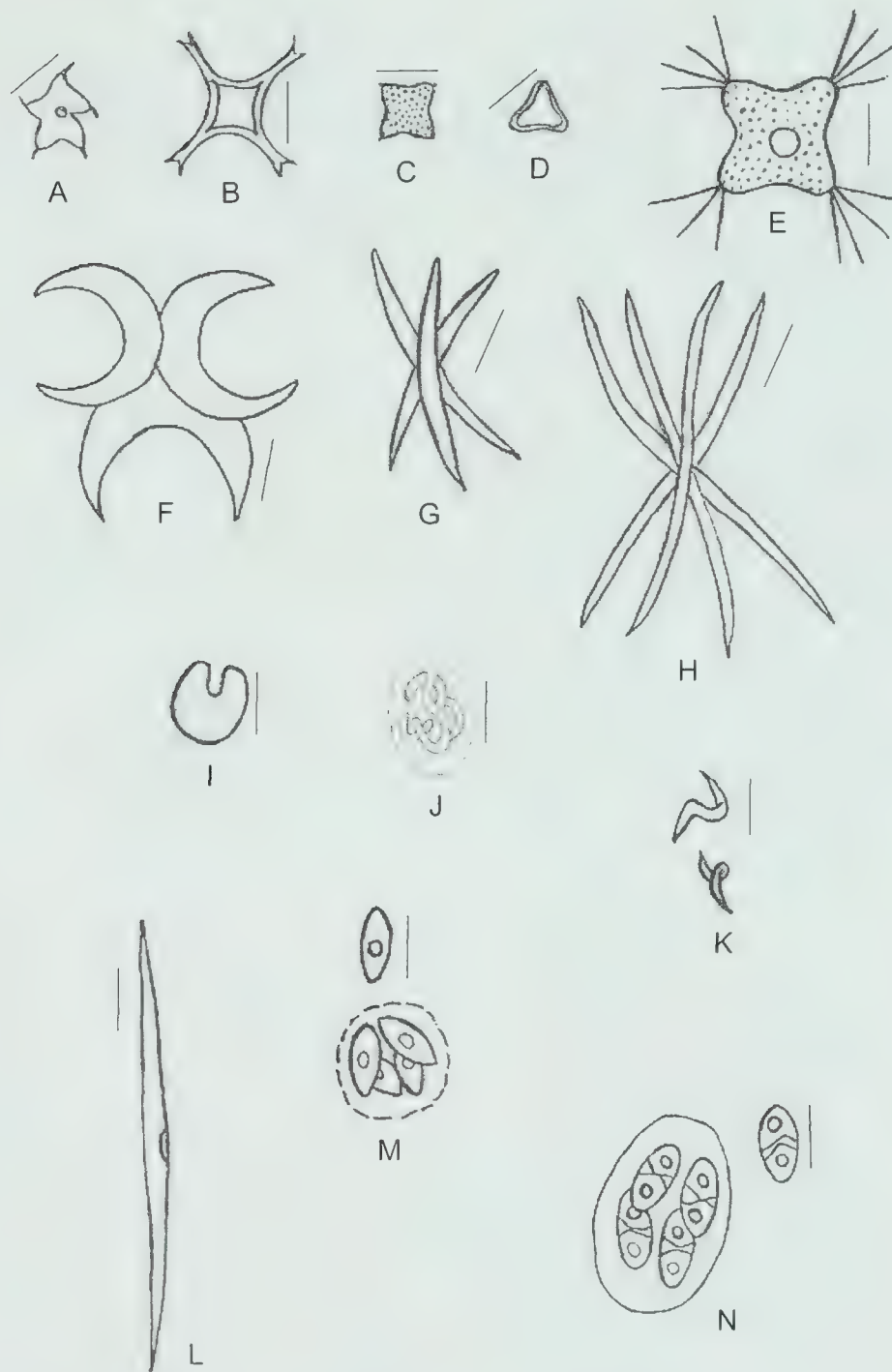


Figure 4 – A, *Tetraedron caudatum* var. *incisum*; B, *Tetraedron hastatum*; C, *Tetraedron minimum*; D, *Tetraedron muticum*; E, *Polyedriopsis spinulosa*; F, *Ankistrodesmus bibraianus*; G, *Ankistrodesmus fusiformis*; H, *Ankistrodesmus falcatus*; I, *Kirchneriella obesa*; J, *Kirchneriella contorta*; K, *Monoraphidium circinale*; L, *Monoraphidium griffithii*; M, *Oocystis parva*; N, *Oocystis* sp. Les traits d'échelle représentent chacun 10 μm .

angle porte trois à quatre soies fines. La cellule est pourvue d'un pyrénioïde et a la membrane ponctuée. Cette description correspond à celle de l'espèce décrite par Bourrelly (1966).

Golenkinia Chodat – Le genre *Golenkinia* présente des cellules sphériques, solitaires, libres, à membrane couverte de longues soies rayonnantes. Son plaste est pariétal, en coupe creuse et pourvu d'un pyrénioïde.

Golenkinia radiata Chodat (fig. 5A) a des cellules sphériques solitaires mais de diamètre compris entre 9 et 10 μm . Comme chez l'espèce décrite par Compère (1976), *G. radiata* présente ici un plaste pariétal couvrant une grande partie de la membrane cellulaire toutefois dans nos échantillons, les cellules sont parfois groupées par trois ou par quatre.

Micractinium Fresen. – Les cellules du genre *Micractinium* sont sphériques ou ellipsoïdales, ornées de longues soies, groupées en cénobes tétraédriques pouvant former des amas plus importants; chaque cellule a un plaste en coupe, avec ou sans pyrénioïde.

M. pusillum Fresen. (fig. 5B) se présente sous forme de cénobe tétraédrique comprenant parfois de nombreuses cellules sphériques à diamètre égal à 6–7 μm et ornées de soies rayonnantes fines et longues. Les plastes sont ici pourvus de pyrénioïde. Les spécimens de nos échantillons présentent un diamètre plus grand que celui des spécimens décrits par Ittis (1972) et qui varie entre 4 et 5 μm .

Spirogyra Link – Le genre *Spirogyra* forme des filaments simples; les cellules renferment deux ou trois plastes rubanés tordus en hélice et portant des pyrénioïdes.

Spirogyra sp. (fig. 5E) est sous forme de filament simple. Les cellules cylindriques, de 65 $\times$ 47 μm , ont deux plastes rubanés tordus en hélice et portant des pyrénioïdes.

Tetrastrum Chodat – Il présente des cénobes plats, formés de 4 cellules plus ou moins disposées en carré ou en croix, toujours ornées d'une ou de plusieurs soies fines et longues; le plaste est pariétal, avec ou sans pyrénioïde.

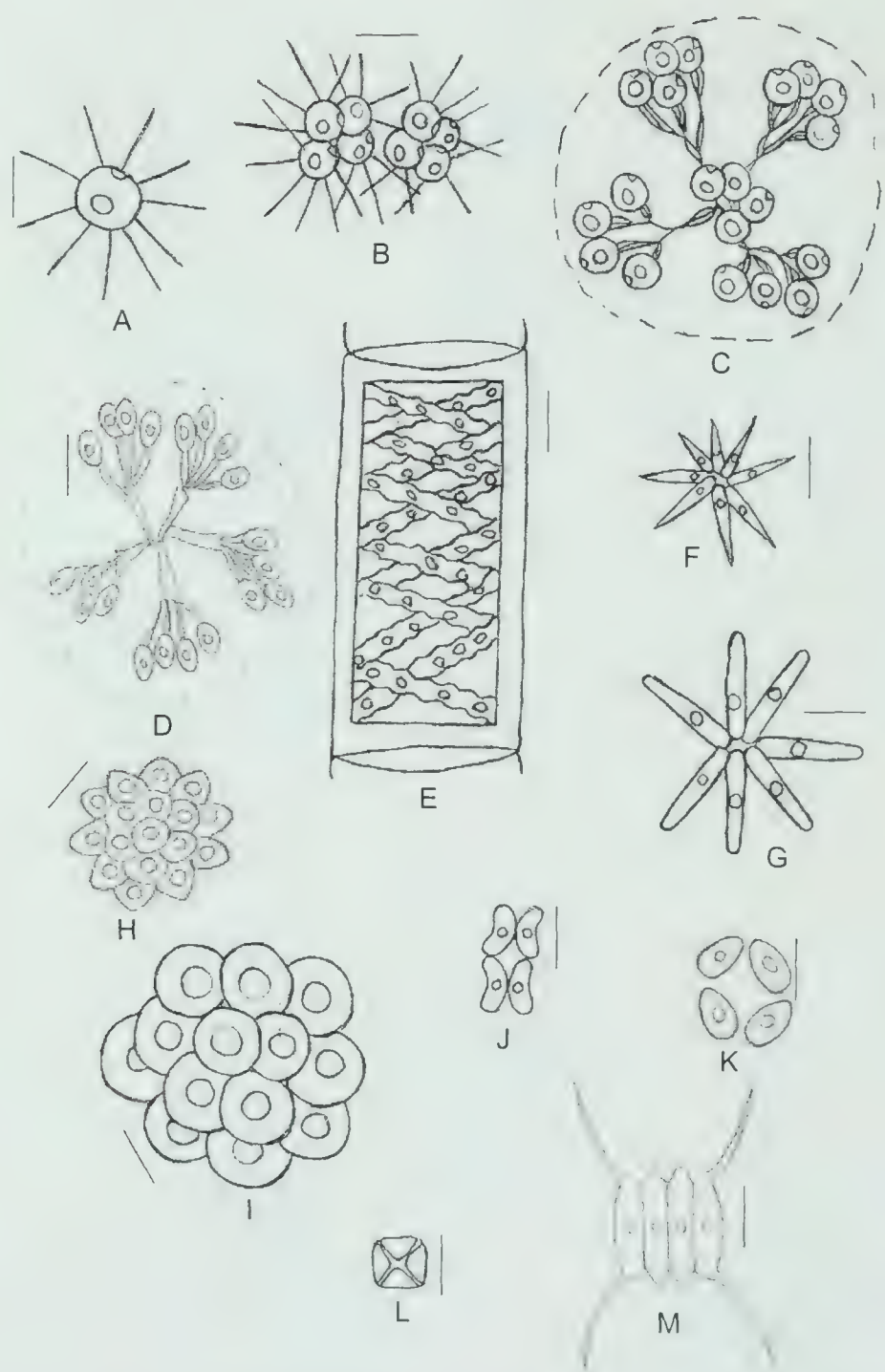


Figure 5 – A, *Golenkinia radiata*; B, *Micractinium pusillum*; C, *Dictyosphaerium pulchellum*; D, *Dictyosphaerium tetrachotomum*; E, *Spirogyra* sp.; F, *Actinastrum aciculare* f. *minimum*; G, *Actinastrum hantzschii*; H, *Coelastrum astroideum*; I, *Coelastrum microporum*; J, *Crucigenia crucifera*; K, *Crucigenia rectangularis*; L, *Crucigenia tetrapedia*; M, *Senedsmus protuberans*. Les traits d'échelle représentent chacun 10 μm .

Tetrastrum staurogeniaeforme (Schröd.) Lemmerm. (fig. 6I) présente un cénobe plat de 4 cellules trapézoïdales disposées en croix et pourvues chacune de 4 ou 5 soies à la surface. Chaque cellule renferme un pyrénoïde et a un diamètre égal à 4 μm correspondant à celui de l'espèce décrite par Compère (1976). Par contre la forme décrite par Iltis (1972) présente des cellules plus grandes de 5 à 7 μm de diamètre qui ne sont pourvues que de deux soies.

Staurostrum Meyen ex Ralfs – Les cellules du genre *Staurostrum* sont solitaires et divisées par un sinus médian plus ou moins profond en deux demi-cellules appelées hémisomates. La vue apicale montre le plus souvent un contour polygonal avec au moins trois angles parfois prolongés par des appendices en forme de bras terminés par des épines; leur membrane peut être lisse, ponctuée, granuleuse épineuse verruqueuse. Ils possèdent généralement un seul plaste central par hémisomate portant un pyrénoïde central.

Staurostrum volans W.West & G.S.West (fig. 6O) présente quatre bras denticulés divergents, bifurqués à l'extrémité. Les hémisomates sont polygonales avec un apex convexe et possèdent un pyrénoïde central. Elle a la même morphologie que l'espèce mentionnée par Thérézien (1986) et Bourrelly & Couté (1986a).

Tetraedron Kütz. – Le genre *Tetraedron* présente des cellules solitaires, de forme très variée mais toujours en coussinets. Les sommets des cellules peuvent présenter des appendices simples ou ramifiés. Leur membrane peut être lisse ou ornée de granulations.

La forme des cellules et le type d'ornementation sont les éléments de discrimination entre les taxons du genre *Tetraedron*.

Tetraedron minimum (A.Braun) Hansg. (fig. 4C) présente une membrane ponctuée contrairement aux autres à membrane lisse. Parmi ces dernières, seules les cellules de *T. muticum* (A.Braun) Hansg. (fig. 4D) qui sont triangulaires

avec des cotés légèrement concaves ne présentent pas d'appendices aux angles.

Si les cellules *T. hastatum* (Reinsch) Hansgirg (fig. 4B) présentent des angles prolongés par un appendice simple bifurqué, celles de *T. caudatum* var. *incisum* Brunth. (fig. 4A) sont légèrement mucronées aux angles.

Ces quatre taxons ont été ainsi mentionnés par Compère (1976).

Ankistrodesmus Corda – Le genre *Ankistrodesmus* est caractérisé par des cellules fusiformes, droites ou légèrement recourbées, parfois sigmoïdes, à apex aigus et regroupées en cénobe fasciculé.

La forme des cellules et de leurs extrémités permettent de différencier les taxons du genre *Ankistrodesmus*.

Les cellules sont fortement recourbées en croissant chez *A. bibraianus* (Reinsch) O.Korshikov (= *Selenastrum bibraianum* Reinsch) (fig. 4F), en aiguilles droites ou légèrement recourbées chez les deux autres taxons. Celles d'*A. falcatus* (Corda) Ralfs (fig. 4H) ont des extrémités très atténuées contrairement à celles de *A. fusiformis* Corda sensu Korshikov (fig. 4G) qui sont peu atténuées.

Kirchneriella Schmidle – Il est caractérisé par des colonies sphériques à ellipsoïdales formées de cellules recourbées en croissant ou contournées-vermiformes, groupées sans ordre dans une gelée commune; le plaste est pariétal, parfois pourvu d'un pyrénioïde.

La forme de la cellule différencie les deux taxons de *Kirchneriella*.

K. contorta (Schmidle) Bohlin (fig. 4J) présente des cellules vermiformes tordues tandis que *K. obesa* (W.West) Schmidle (fig. 4I) à contour circulaire présente une fente en U et est obtuse aux deux extrémités.

K. obesa que nous avons récoltée est formée de cellules solitaires. Ceci peut s'expliquer par l'agitation du milieu. Ces cellules (5 µm) sont identiques à celles observées par Pérez et al. (2002) même si ces dernières (1,6–4 µm) sont regroupées dans une gelée.

Quant à *K. contorta*, le diamètre de ses cellules (2 µm) est égal à celui des cellules mentionnées par Compère (1976).

Monoraphidium Komárk.-Legn. – Ce sont des cellules solitaires, cylindriques ou fusiformes, droites, recourbées en croissant, sigmoïdes ou vermiformes, souvent terminées par une longue pointe; leur plaste est pariétal, avec ou sans pyrénioïde.

La forme des cellules permet de distinguer les deux espèces de *Monoraphidium* rencontrées.

Les cellules sont fusiformes et aiguës aux extrémités chez *Monoraphidium griffithii* (Berk.) Komárk.-Legn. (fig. 4L) et *M. circinale* (Nygaard) Nygaard (fig. 4K). Elles sont cependant droites (65 × 2,5 µm) chez *M. griffithii* et irrégulièrement tordues (12 × 2 µm) chez *M. circinale*.

M. griffithii présente les mêmes caractéristiques que les spécimens mentionnés par Compère (1976) et par Pérez et al. (2002). *M. circinale* aussi correspond bien aux spécimens mentionnés par Bourrelly & Couté (1986b).

Dictyosphaerium Nägeli – Le genre *Dictyosphaerium* se présente sous forme de colonie composée de cellules sphé-

riques ou ellipsoïdales réunies par 4 par des tractus gélatineux et pourvues de plastes en coupe et de pyrénioïde.

Les deux taxons observés du genre *Dictyosphaerium* se distinguent par la forme de leurs cellules. Celles-ci sont sphériques chez *D. pulchellum* H.C.Wood (fig. 5C) et ellipsoïdales chez *D. tetrachotomum* Printz (fig. 5D). Le diamètre des cellules est respectivement de 5–6 µm et 6–7 µm. Les cellules de *D. tetrachotomum* de nos échantillons ont des diamètres légèrement plus grands que celles de l'espèce rencontrée dans les échantillons de Bourrelly & Couté (1986b). Par contre, les cellules de *D. pulchellum* ont les mêmes dimensions que celles données par Compère (1976).

Oocystis A.Braun – Ce sont des cellules globuleuses ellipsoïdales ou ovoïdes, solitaires ou par groupe de deux à seize contenues dans la membrane-mère dilatée. La membrane cellulaire est le plus souvent épaissie aux deux pôles; les cellules peuvent être pourvues d'un ou de plusieurs plastes, avec ou sans pyrénioïde.

Les cellules des taxons rencontrés sont solitaires ou groupées par quatre dans une enveloppe-mère. Elles se différencient par la forme de la cellule et le type de plaste. Les cellules d'*Oocystis parva* W.West & G.S.West (fig. 4M) sont ellipsoïdales (11–12 × 4–5 µm) et présentent un plaste unique avec pyrénioïde contrairement aux cellules d'*Oocystis* sp. (fig. 4N) qui sont ovoïdes (11–12 × 5 µm) et à plaste divisé en trois avec pyrénioïde.

Les cellules d'*Oocystis parva* ont les mêmes caractéristiques que celles des spécimens rencontrés par Compère (1976).

Actinastrum Lagerh. – Le genre *Actinastrum* est caractérisé par des cellules en cénobe étoilé rayonnant sur plusieurs plans mais leur forme permet de différencier les taxons rencontrés. Chaque cellule renferme un plaste pourvu d'un pyrénioïde.

A. aciculare f. *minimum* (Huber-Pestalozzi) Compère (fig. 5F) présente des cellules lancéolées arrondies à la base et effilées au sommet tandis qu'*A. hantzschii* Lagerh. (fig. 5G) a des cellules cylindriques tronquées au sommet. Les dimensions sont respectivement de 12 × 2–3 µm et 16 × 2,5–3 µm.

Ces deux taxons présentent les mêmes caractéristiques que celles rencontrées par Compère (1976).

Coelastrum Nägeli – Ce genre forme des cénobes sphériques ou subsphériques creux, c'est-à-dire dont les cellules sont disposées à la surface de la sphère. Elles peuvent être collées ou reliées entre elles par des appendices plus ou moins longs; le plaste renferme un pyrénioïde.

La forme des cellules permet de différencier les deux taxons rencontrés.

Les cellules sont sphériques chez *C. microporum* Nägeli (fig. 5I) et ovoïdes chez *C. astroideum* De Not. (fig. 5H) et le diamètre est respectivement de 11–13 µm et de 6–7 µm.

C. microporum est identique aux spécimens mentionnés par Compère (1976) et dont le diamètre des cellules varie entre 4 et 27 µm.

Crucigenia Morren – Le genre *Crucigenia* est sous forme de cénobe plat de 4 cellules et présente un méat central. La

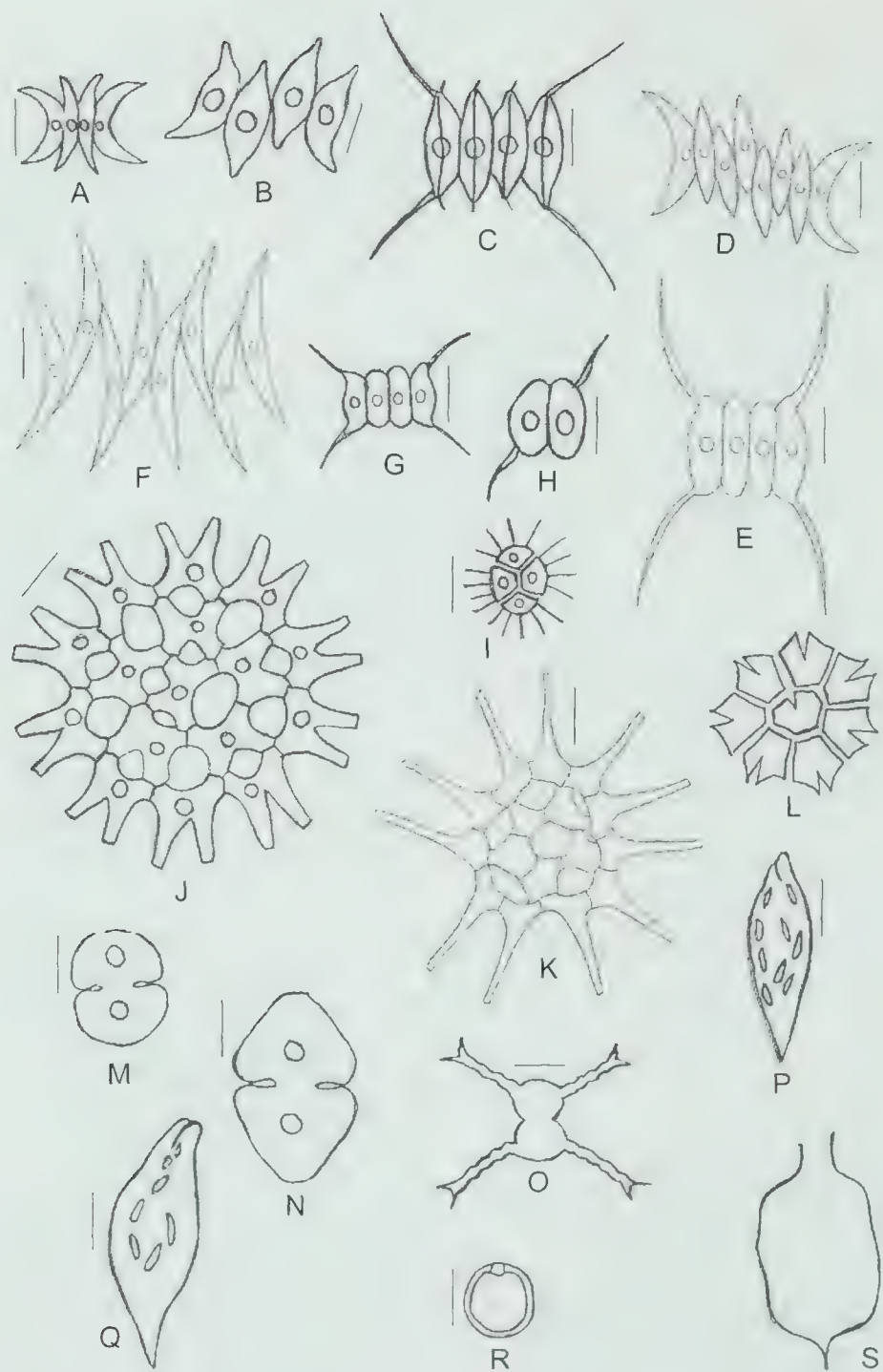


Figure 6 – A, *Scenedesmus acuminatus*; B, *Scenedesmus acutus* f. *alternans*; C, *Scenedesmus carinatus*; D, *Scenedesmus dimorphus*; E, *Scenedesmus quadricauda* var. *longispina*; F, *Scenedesmus javanensis*; G, *Scenedesmus quadricauda*; H, *Scenedesmus quadricauda* var. *bicaudatus*; I, *Tetrastrum staurogeniaeforme*; J, *Pediatrum duplex*; K, *Pediatrum clathratum*; L, *Pediatrum tetras*; M, *Cosmarium constrictum* f. *minus*; N, *Cosmarium granatum*; O, *Staurostrum volans*; P, *Euglena* sp.1; Q, *Euglena* sp.2; R, *Trachelomonas volvocina*; S, *Strombomonas verrucosa*. Les traits d'échelle représentent chacun 10 μ m.

forme du cénobe et celle des cellules différencient les différents taxons.

Le cénobe de *C. crucifera* (Wolle) Kuntze (fig. 5J) est rhomboïdal contrairement à *C. tetrapedia* (Kirchn.) Kuntze (fig. 5L) et *C. rectangularis* (Nägeli) W.B.Turner (fig. 5K) qui présentent respectivement des cénobes plus ou moins carrés et des cénobes plus ou moins rectangulaires. Les cellules ont une forme réniforme chez *C. crucifera*, triangulaire arrondie chez *C. tetrapedia* et ovoïde chez *C. rectangularis*; leur diamètre est respectivement 2–2.5 μ m, 7 μ m et 6 μ m. Ces trois taxons ont été mentionnés par Compère (1976) avec les mêmes caractéristiques.

Scenedesmus Meyen – Leurs cénobes sont plats, formés de deux, quatre ou huit cellules disposées côte à côte en série linéaire, plus rarement en deux rangées alternantes; chaque cellule a un seul plaste pariétal pourvu d'un pyrénioïde. Les cellules sont souvent ornementées d'épines, d'aiguillons, de

pores, de côtes longitudinales, les cellules marginales du cénobe ayant souvent une ornementation différente de celles du centre.

La forme du cénobe, des cellules et le type d'ornementation permettent de distinguer les différentes espèces de *Scenedesmus* rencontrées.

Parmi les taxons identifiés, trois (*Scenedesmus acutus* f. *alternans* Hortob., *S. dimorphus* (Turpin) Kütz. et *S. javanensis* Chodat) présentent des cellules disposées en deux séries alternantes contrairement aux autres dont les cénobes sont linéaires.

Tous les taxons à cénobes linéaires sont pourvus d'aiguillons sauf *S. acuminatus* (Lagerh.) Chodat (fig. 6A) dont le cénobe est composé de quatre cellules fusiformes à extrémités pointues ayant la même forme que celle décrite par Pérez et al. (2002). Cependant, seule *S. quadricauda* var.

bicaudatus Hansg. (fig. 6H) présente deux aiguillons disposés en diagonale. Les autres taxons ont des cénobes pourvus de quatre aiguillons, un à chaque pôle. Parmi ces derniers, on a noté la présence de côte longitudinale se terminant par une petite épine chez *S. carinatus* (Lemmerm.) Chodat (fig. 6C).

Les cénobes de *S. quadricauda* (Turpin) Bréb. (fig. 6G) et de *S. quadricauda* var. *longispina* (Chodat) G.M.Sm. (fig. 6E) sont formés de quatre cellules cylindriques dont les deux internes sont arrondies aux pôles contrairement à *S. protuberans* F.E.Fritsch & M.F.Rich (fig. 5M) dont les cellules sont cylindriques à fusiformes ($30 \times 5 \mu\text{m}$) et atténuées aux pôles. Les dimensions des cellules internes sont de $12 \times 3 \mu\text{m}$ chez *S. quadricauda* et de $23 \times 6\text{--}7 \mu\text{m}$ chez *S. quadricauda* var. *longispina*.

S. acutus f. *alternans* (fig. 6B) a un cénobe formé de quatre cellules ellipsoïdales à extrémités obtuses contrairement à *S. dimorphus* et à *S. javanensis*. Ces deux dernières présentent des cénobes de huit cellules qui sont fusiformes chez *S. javanensis* (6F), le pôle d'une cellule étant conné au milieu du côté de la cellule suivante, alors que chez *S. dimorphus* (fig. 6D) les internes sont ellipsoïdales à fusiformes, les externes plus ou moins courbées en croissant vers l'extérieur.

Pediastrum Meyen – Il présente des cénobes plats, circulaires ou ovales, parfois irréguliers. Ses cénobes sont formés de cellules organisées en disque étoilé dont les cellules marginales n'ont pas le même aspect que les cellules centrales et présentent une à quatre cornes. Les cénobes peuvent présenter des méats. Leurs membranes peuvent être lisses, granuleuses, verruqueuses ou réticulées; les plastes sont pariétaux et contiennent un gros pyrénioïde.

La forme du cénobe, la présence ou l'absence de méats intercellulaires et le nombre de cornes par cellule marginale sont les éléments de discrimination entre les taxons du genre *Pediastrum*.

Chez *P. tetras* (Ehrenb.) Ralfs (fig. 6L), le cénobe quadrangulaire plein est formé de quatre ou huit cellules; les marginales sont profondément incisées et pourvues de deux cornes bifurquées contrairement aux autres espèces. L'espèce est identique à celle mentionnée par Pérez et al. (2002).

Le cénobe en disque étoilé perforé (avec méats intercellulaires) se rencontre chez *P. clathratum* (Schröt.) Lemmerm. (fig. 6K) et *P. duplex* Meyen (fig. 6J) mais les cellules marginales sont pourvues d'une seule corne chez la première et de deux chez la deuxième.

La description de *P. clathratum* correspond bien à celle donnée par Iltis (1972).

Cosmarium Corda ex Ralfs – Leurs cellules sont solitaires, rarement en courtes chaînes, et divisées en deux hémisomates. Ces derniers ont des formes très variables mais ne sont jamais découpées en lobes ni incisées aux pôles. Leur membrane peut être lisse, ponctuée, granuleuse, verruqueuse, épineuse ou diversement ornementée mais jamais ornée d'une ou plusieurs fortes épines latérales; leurs plastes, parfois nombreux, sont pariétaux et renferment un ou plusieurs pyrénioïdes.

La forme des hémisomates permet de distinguer les deux taxons de *Cosmarium* rencontrés.

C. constrictum f. *minus* F.E.Fritsch & Rich (fig. 6M) présente un hémisomate semi-circulaire de $15 \mu\text{m}$ en diamètre (l'isthme est de $4 \mu\text{m}$) contrairement à *C. granatum* Bréb. ex Ralfs (fig. 6N) dont les hémisomates triangulaires sont légèrement convexes vers la base et ont un apex plat de $15 \mu\text{m}$ de diamètre (l'isthme est de $7 \mu\text{m}$). Chacun de ces hémisomates contient un pyrénioïde. Ces descriptions correspondent à celles rencontrées par Compère (1977).

Morphologie des Euglénophytes rencontrés

Trois genres d'Euglénophytes ont été rencontrés dans nos échantillons. Ce sont les genres *Euglena* Ehrenb., *Trachelomonas* Ehrenb. et *Strombomonas* Deflandre qui comportent tous des cellules solitaires flagellées. Mais les taxons que nous avons observés ne présentent plus leurs flagelles; cela peut être dû à la fixation au formol.

Le genre *Euglena* comporte des cellules fusiformes parfois globuleuses, non enfermées dans une logette (ou thèque). Leur cuticule est souvent ornementée de stries hélicoïdales. Il existe un ou plusieurs plastes verts avec ou sans pyrénioïde. Dans ce genre, deux taxons (*Euglena* sp.1 et *Euglena* sp.2) non encore identifiés sont rencontrés.

Euglena sp.1 (fig. 6P) est obtuse au pôle antérieur et effilée au pôle postérieur; elle présente de nombreux grains de paramylon arrondis et dispersés dans le cytoplasme. Ses dimensions sont $36 \times 12 \mu\text{m}$.

Euglena sp.2 (fig. 6Q) présente une cellule ovoïde de $46 \times 14 \mu\text{m}$ dont le pôle antérieur est terminé par une petite pointe. Les plastes sont nombreux et discoïdes; le paramylon est en grains arrondis dispersés dans le cytoplasme.

Contrairement au genre *Euglena*, les genres *Trachelomonas* et *Strombomonas* ont des cellules contenues dans une logette.

La logette des cellules du genre *Strombomonas* peut être lisse ou rugueuse. Les cellules sont atténuées, formant un col au pôle antérieur. Elles sont obtuses et portent une queue au pôle postérieur. *S. verrucosa* (Daday) Deflandre (fig. 6S), avec $33 \mu\text{m}$ de long sur $23 \mu\text{m}$ de large, présente une membrane rugueuse; le col est tronqué obliquement, le pôle postérieur terminé par une courte queue. Le spécimen observé correspond à celui observé par Iltis (1972).

Le genre *Trachelomonas* présente une thèque ou logette brune de forme ellipsoïdale, ovoïde ou sphérique, souvent ornée de pores, de fossettes, d'épines, de verrues ou d'aiguillons; cette thèque est percée d'un pore qui laisse passer le flagelle locomoteur de la cellule contenue à l'intérieur. *T. volvocina* (Ehrenb.) Ehrenb. (fig. 6R) est sphérique et à membrane lisse. Les cellules ont des diamètres de $9\text{--}10 \mu\text{m}$, comparables à ceux donnés par Compère (1970) mais inférieurs à ceux d'Iltis (1972) dont les diamètres varient entre 16 et $18 \mu\text{m}$.

A la suite de cette étude morphologique, une clé de détermination pour l'ensemble des genres et espèces de Cyanobactéries et de microalgues récoltées dans le PNOD est proposée.

Clé des cyanobactéries et microalgues du PNOD

1. Procaryotes.....	2: CYANOBACTERIES
1'. Eucaryotes.....	29: MICROALGUES
2. Thalle unicellulaire solitaire.....	3
2'. Thalle pluricellulaire.....	4
3. Cellules sphériques de 3,5 µm de diamètre.....	<i>Synechocystis aqualitis</i>
3'. Cellules cylindriques de 3 µm de diamètre.....	<i>Synechococcus ambiguus</i>
4. Thalle pluricellulaire colonial.....	5
4'. Thalle pluricellulaire filamenteux.....	13
5. Présence d'une gaine gélatineuse individuelle.....	6: <i>Chroococcus</i>
5'. Absence de gaine gélatineuse individuelle.....	8
6. Colonie renfermant 2 cellules sphériques.....	<i>Chroococcus minor</i>
6'. Colonie renfermant 4 cellules subsphériques.....	7
7. Cellules de 6 µm de diamètre.....	<i>Chroococcus minutus</i>
7'. Cellules de 10 µm de diamètre.....	<i>Chroococcus limneticus</i>
8. Colonie tabulaire plate à cellules subsphériques.....	<i>Merismopedia tenuissima</i>
8'. Colonie non tabulaire.....	9
9. Cellules sphériques ou subsphériques.....	10: <i>Microcystis</i>
9'. Cellules ellipsoïdales de 3–4 µm de diamètre.....	<i>Aphanothece elabens</i>
10. Cellules à distribution éparses.....	<i>Microcystis delicatissima</i>
10'. Cellules à distribution dense.....	11
11. Cellules pourvues de pseudovacuoles.....	<i>Microcystis aeruginosa</i>
11'. Cellules dépourvues de pseudovacuoles.....	12
12. Cellules de 5 µm de diamètre.....	<i>Microcystis densa</i>
12'. Cellules de 3 µm de diamètre.....	<i>Microcystis incerta</i>
13. Présence de gaine.....	14: <i>Lyngbya</i>
13'. Absence de gaine.....	15
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73'. Cellule de $46 \times 14 \mu\text{m}$	<i>Euglena</i> sp.2

Composition taxonomique

L'observation des différents échantillons a permis d'inventorier au niveau du PNOD les différents taxons représentés dans l'appendice électronique.

Cette étude a révélé la présence de 74 taxons répartis en 34 genres et douze familles dans la microflore du Parc National des Oiseaux du Djoudj. Ces espèces appartiennent aux embranchements des Cyanobactéries, des Chlorophytes et des Euglénophytes suivant la classification de Bourrelly (1966, 1968, 1970).

Les Cyanobactéries comprennent trois familles regroupant treize genres et 28 taxons. Les plus représentées sont les Chroococcaceae et les Oscillatoriaceae avec respectivement 14,9% et 13,5%. Les Nostocaceae viennent en troisième position avec 9,5%. Ces résultats confirment les travaux de Ba et al. (2006) qui ont inventorié 22 taxons de Cyanobactéries appartenant à quinze genres et trois familles (Chroococcaceae, Oscillatoriaceae et Nostocaceae).

Quant aux genres, *Anabaena* est le plus représentatif avec cinq taxons, suivi des genres *Microcystis* et *Pseudanabaena* ayant chacun quatre taxons et du genre *Chroococcus* avec trois espèces. Les genres *Raphidiopsis*, *Komvophoron* et *Lyngbya* sont représentés chacun par deux espèces alors que chez les genres *Aphanothece*, *Merismopedia*, *Synechocystis*, *Synechococcus*, *Arthrospira* et *Oscillatoria* une seule

espèce a été recensée. Cette dominance du genre *Anabaena* a été constatée dans les travaux de Berger et al. (2005) car sur les 76 taxons rencontrés, douze appartiennent à ce genre. Cela peut être lié à une pauvreté en azote.

S'agissant des microalgues, elles regroupent 46 taxons répartis dans 21 genres et neuf familles.

Les familles des Chlorophytes sont dominées par celle des Scenedesmaceae, avec 23% des taxons. Elle est suivie des familles des Oocystaceae (12,2%) et des Chlorococcaceae (6,8%). Les familles des Hydrodictyaceae et des Desmidiaceae forment chacune 4% de l'ensemble des taxons. Les Micractiniaceae et les Dictyosphaeriaceae ont le même pourcentage (2,7%). Les Zygnemataceae sont les moins représentées avec seulement 1,4%.

Au niveau des genres, *Scenedesmus* est nettement dominant avec neuf taxons, puis viennent le genre *Tetraedron* (quatre taxons) et les genres *Ankistrodesmus*, *Pediastrum* et *Crucigenia* avec trois taxons. Les genres *Kirchneriella*, *Monoraphidium*, *Oocystis*, *Dictyosphaerium*, *Actinastrum*, *Coelastrum*, et *Cosmarium* ont chacun deux taxons. Les autres genres sont représentés par un seul taxon.

Concernant les Euglénophytes, elles ne sont représentées ici que par la famille des Euglenaceae qui forme 5,4% des taxons avec le genre *Euglena* qui est le plus représentatif.

Les genres *Strombomonas* et *Trachelomonas* sont représentés chacun par un taxon.

Richesse spécifique

En termes de richesse spécifique, les Chlorophytes constituent le groupe le plus important avec 56,8% des taxons, suivies des Cyanobactéries formant les 37,8%. Les Euglénophytes sont moins représentées avec seulement 5,4%.

Cette prédominance des Chlorophytes et des Cyanobactéries pourrait s'expliquer par l'apport de phosphore provenant des déjections des oiseaux car les eaux sont jaunes et très turbides. Cela peut être confirmé par la prolifération de *Microcystis aeruginosa* au niveau des sites Nichoir Pélican 1 et Nichoir Pélican 2. Cette espèce, selon Iltis (1973), forme des peuplements très denses dans les eaux douces relativement riches en sels dissous. En plus, le faible pourcentage des Desmidiacées peut confirmer cette richesse en sels dissous car selon toujours Iltis (1973), la plupart de ces espèces sont acidophiles, ce qui explique leur rareté dans les eaux alcalines riches en sels dissous.

En termes de nombre de taxons décrits, la comparaison de nos résultats à ceux antérieurs révèle la présence de 23 taxons nouveaux pour le Sénégal. Il s'agit de:

- sept taxons de Cyanobactéries (*Chroococcus minor*, *Microcystis delicatissima*, *Synechococcus ambiguus*, *Lyngbya orientalis*, *Oscillatoria foreau*, *Pseudanabaena africana*, et *Rhaphidiopsis mediterranea*);
- quinze taxons de Chlorophytes (*Tetraedron hastatum*, *Tetraedron caudatum* var. *incisum*, *Polyedriopsis spinulosa*, *Ankistrodesmus bibrainus*, *Monoraphidium circinale*, *Golenkinia radiata*, *Actinastrum aciculare* f. *minimum*, *Crucigenia crucifera*, *Scenedesmus acutus* f. *alternans*, *Scenedesmus carinatus*, *Scenedesmus javanensis*, *Scenedesmus quadricauda* var. *longispina*, *Scenedesmus quadricauda* var. *bicaudatus*, *Tetrastrum staurogeniaeforme*, *Cosmarium constrictum* f. *minus*);
- un taxon d'Euglénophyte (*Strombomonas verrucosa*).

Affinités biogéographiques

Sur les 74 taxons déterminés, 66,2% (49 taxons) sont cosmopolites, 5,4% (quatre taxons) subcosmopolites. Donc 71,6% de l'ensemble des taxons ont une très large distribution. Les taxons tropicaux les représentent 8,1% (six taxons) tandis que celles d'affinité africaine ne sont que quatre, c'est-à-dire 5,4% et onze taxons (14,9%), ont une biogéographie inconnue. Cela pourrait s'expliquer par une diversité des conditions écologiques et la fréquentation de cet écosystème par des oiseaux migrants. En effet, de septembre à avril, trois millions d'oiseaux migrants traversent la région. Environ 300 espèces d'oiseaux ont été recensées dans ce parc (MEPN, 1997). En janvier 2006, 21925 pélicans, 22067 ardeidés, 437 cigognes, 5381 spatules, 21919 flamants, 3412 ibis et 146 grues couronnées ont été dénombrées dans le delta du Sénégal (Trollet et al. 2007). En janvier 2007, 67.560 limicoles dont 17.557 échasses blanches, 11.423 combattants et 5.613 barges à queue noire ont été recensés (Trollet et al. 2008).

CONCLUSION

Grâce à l'étude descriptive, des clés de détermination des genres et espèces de Cyanobactéries et de microalgues ont été élaborées pour faciliter la reconnaissance des différents taxons rencontrés dans le Parc National des Oiseaux du Djoudj

L'inventaire systématique a permis de recenser 74 taxons répartis en 34 genres et douze familles. En termes de taxons, les microalgues sont dominantes avec 62,2% (56,8% de Chlorophytes et 5,4% d'Euglénophytes), suivies des Cyanobactéries représentant les 37,8%. La famille des Scenedesmaceae avec 23,0% des taxons, est prédominante chez les microalgues, suivie de la famille des Oocystaceae avec 12,2%. Le genre *Scenedesmus* est nettement dominant avec neuf taxons. Chez les Cyanobactéries, les familles les plus représentées sont les Chroococcaceae et les Oscillatoriaceae avec respectivement 14,9% et 13,5% tandis que le genre dominant est *Anabaena* avec cinq taxons.

Sur le plan biogéographique, les résultats obtenus montrent une prédominance des taxons cosmopolites et subcosmopolites qui représentent 71,6% des espèces inventoriées.

Parmi ces 74 taxons, 23 (sept Cyanobactéries, quinze Chlorophytes et une Euglénophyte) sont mentionnés pour la première fois au Sénégal et viennent s'ajouter à la liste des taxons connues de ce pays.

Ces résultats obtenus confirment que le PNOD constitue un site de grande biodiversité et soulignent à nouveau l'intérêt de ce Parc dans la préservation de la diversité régionale.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible au format pdf sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> > SBB50 > dossier 566) et consiste en une liste des taxons récoltés dans le PNOD, avec leur répartition (groupe, famille).

REMERCIEMENTS

Cette étude a été réalisée dans le cadre du programme Sud Expert Plantes, sous le numéro de projet 316.

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Manuscript received 27 Oct. 2010; accepted in revised version 4 Jul. 2011.

Communicating Editor: Jérôme Degreel.



Diversity of ferns and lycophytes in São Tomé and Príncipe: an updated checklist

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Background – São Tomé and Príncipe harbour a total of 156 taxa of ferns and lycophytes, 143 in São Tomé and 77 in Príncipe. Of these, thirteen are endemic, 47 are rare and sixteen are very rare or even extinct.

Aim – This article presents an updated checklist with relevant synonyms of the ferns and lycophytes of these small islands in the Gulf of Guinea.

Key words – São Tomé and Príncipe, ferns, lycophytes, checklist, diversity.

INTRODUCTION

The flora of the four islands in the Gulf of Guinea (Bioko, São Tomé, Príncipe and Annobon) has been treated in separate revisions, reflecting the political boundaries of these islands. São Tomé and Príncipe form a country, while Bioko (formerly known as Fernando Po) and Annobon are included in Equatorial Guinea. The flora of Bioko and Annobon is covered by the *Flora de Guinea Ecuatorial* (Velayos et al. 2008). For São Tomé and Príncipe an updated catalogue of the flowering plants was recently published (Figueiredo et al. 2011).

The fern and lycophyte flora of Bioko and Annobon have been recently revised (Velayos et al. 2008). The ferns and lycophytes of Bioko had been previously treated by Benl (1978, 1980, 1982, 1988, 1991) who provided descriptions of and keys to the taxa. An update of the Annobon fern and lycophyte flora was produced by Figueiredo et al. (2009).

The revision of the ferns and lycophytes of São Tomé and Príncipe was undertaken by Alston (1944) with two later additions (Alston 1958, 1959). This revision was only updated about fifty years later, resulting then in a list of 156 taxa (Figueiredo 1998).

Several additions to the knowledge of the fern and lycophyte flora of São Tomé and Príncipe were subsequently published. In 2001, new data became available for ten species that had not been recorded in the islands for 40–100 years (Figueiredo 2001). At the same time, the rarity and conservation status of 22 taxa (thirteen endemic and nine non-endemic) was assessed by Figueiredo & Gascoigne (2001). IUCN Red List categories of threat were proposed for these

taxa, with 8 taxa proposed to be considered Critically Endangered, three Endangered and eleven Vulnerable. So far, none of these taxa is listed in the Red List (IUCN 2010). Specific measures were also suggested to conserve these rare pteridophytes, but they have not been implemented.

A guide to the identification of the ferns and lycophytes of São Tomé and Príncipe (Figueiredo 2002) provided descriptions, keys and data on all localities where each taxon was recorded. Based on their representation in herbaria, some taxa were considered rare and some possibly extinct locally (when no collections were known from the last 100 years).

In 2008, Figueiredo & Roux reviewed the ferns and lycophytes restricted to the lowland rainforests of São Tomé and Príncipe, assessing their distribution, rarity, and possible threats. Twelve lowland species were then considered locally rare and measures to protect them were proposed. It was concluded that there is a need to conserve some lowland areas in São Tomé and three areas were proposed for conservation.

METHODOLOGY

The present list updates the nomenclature of the fern and lycophyte flora of São Tomé and Príncipe following Roux (2009). The synonyms listed are only those names that were used in the recent literature for these islands. Vouchers are cited in previous literature (Figueiredo 1998, 2001, Figueiredo & Gascoigne 2001, Figueiredo & Roux 2008).

RESULTS

The present updated checklist brings the fern and lycophyte diversity up to 156 taxa in São Tomé and Príncipe, 143 in São Tomé and 77 in Príncipe. There are 34 nomenclatural changes in reference to the previous list (Figueiredo 1998). Twelve taxa were considered endemic in 1998, the current figure being thirteen. Forty-seven taxa are rare and should not be collected.

CHECKLIST

(^E = Endemic; ^R = Rare; * = naturalised; ST = São Tomé; P = Príncipe)

Abrodictyum C.Presl (Hymenophyllaceae)

Abrodictyum rigidum (Sw.) Ebiara & Dubuisson

= *Trichomanes rigidum* Sw.

ST, P. Mostly terrestrial in secondary forest up to 700 m in ST and 600 m in P.

Acrostichum L. (Parkeriaceae)

Acrostichum aureum L.

ST, P. Mangroves and swamps, in coastal areas.

Adiantum L. (Adiantaceae)

Adiantum lunulatum Burm.f.

= *Adiantum philippense* L.

ST. Lowland forest up to 600 m.

* *Adiantum raddianum* C.Presl

ST, P. Cultivated and naturalised, in forest at 490–1800 m.

^R *Adiantum soboliferum* Hook.

= *Adiantum mettenii* Kuhn

ST. Lowland forest up to 600 m.

Adiantum vogelii Mett. ex Keyserl.

P. In low altitude, coastal areas.

Alsophila R.Br. (Cyatheaceae)

^E *Alsophila camerooniana* (Hook.) R.M.Tryon var. *currorii* (Holtum) J.P.Roux

= *Cyathea camerooniana* Hook. var. *currorii* Holtum

P. Tree fern in lowland forest at 60–350 m.

Alsophila manniana (Hook.) R.M.Tryon

Cyathea manniana Hook.

ST. Tree fern in mountain forest at 1000–2020 m.

^E *Alsophila welwitschii* (Hook.) R.M.Tryon

Cyathea welwitschii Hook.

ST. Tree fern in mountain forest, rarely in lowland forest, at 200–1850 m.

Anthrophyum Kaulf. (Adiantaceae)

^R *Anthrophyum immersum* (Bory ex Willd.) Hook. & Baker

ST, P. Epiphyte in lowland forest and mountain forest at 10–1700 m.

Anthrophyum mannianum Hook.

ST. Mostly epiphyte in lowland forest and mountain forest at 200–2000 m.

Arthropteris J.Sm. ex Hook.f. (Tectariaceae)

Arthropteris monocarpa (Cordem.) C.Chr.

ST, P. Mostly epiphyte in mountain forest at 1000–1987 m in ST, c. 500 m in P. Collected once at 80 m in ST.

Arthropteris orientalis (J.F.Gmel.) Posth.

ST, P. Epiphyte or terrestrial in lowland forest and mountain forest at 300–1900 m in ST. Collected once in P at 60 m.

Arthropteris palisotii (Desv.) Alston

ST. Lowland forest at 80–760 m.

Asplenium L. (Aspleniaceae)

Asplenium aethiopicum (Burm.f.) Bech. subsp. *aethiopicum*

ST. Epiphyte in mountain forest at 1200–1987 m.

Asplenium africanum Desv.

ST, P. Epiphyte in lowland forest up to 350 m.

Asplenium anisophyllum Kunze

ST. Epiphyte or terrestrial in mountain forest at 1200–1800 m.

Asplenium barteri Hook.

ST, P. Epiphyte in lowland forest at 100–450 (–800) m.

Asplenium biafranum Alston & F.Ballard ex F.Ballard

ST. Mostly epiphyte in mountain forest at 1000–2020 m.

^R *Asplenium cuneatum* Lam.

ST. Collected only once, at 1200 m; it could be extinct in ST.

Asplenium currorii Hook.

ST, P. Epiphyte in mountain forest at 550–1800 m.

Asplenium dregeanum Kunze

ST. Epiphyte or terrestrial in mountain forest at 850–2020 m.

Asplenium emarginatum P.Beauv.

ST. Terrestrial in lowland forest at 200–800 m.

Asplenium erectum Bory ex Willd.

ST. Epiphyte or terrestrial in mountain forest at 1200–1850 m.

^E *Asplenium eurysorum* Hieron.

ST, P. Epiphyte or terrestrial in mountain forest, lowland forest and secondary forest at 160–1987 m.

^{R E} *Asplenium exhaustum* (H.Christ) Alston

ST. Collected only three times at Pico and at 300 m, the last collection dating from 1956.

^R *Asplenium formosum* Willd.

ST. Epiphyte collected only once in lowland forest, in the 1950s.

^R *Asplenium friesiorum* C.Chr.

ST. Epiphyte or terrestrial in mountain forest, collected only at Pico.

Asplenium hypomelas Kuhn

ST. Epiphyte or terrestrial in mountain forest and secondary forest at 1150–1800 m.

Asplenium inaequilaterale Bory ex Willd.

ST. Mostly terrestrial in mountain forest at 750–1430 m.

- ^R *Asplenium lividum* Mett. ex Kuhn
ST. Epiphyte or terrestrial, collected only three times at 600–900 m.
- ^R *Asplenium longicauda* Hook.
P. Epiphyte or terrestrial in lowland forest at 60–350 m.
- ^R *Asplenium megalura* Hieron.
= *Asplenium megalura* Hieron. var. *molleri* (Hieron.) Tardieu
ST. Epiphyte or terrestrial in mountain forest at 870–1430 m.
- ^R *Asplenium nigritianum* Hook.
ST, P. Collected only twice; it could be extinct in ST and P.
- Asplenium sandersonii* Hook.
ST. Mostly epiphyte in mountain forest and lowland forest at 400–1950 m.
- Asplenium unilaterale* Lam.
ST, P. Epiphyte or terrestrial in mountain forest at 850–1900 m.
- Asplenium variabile* Hook.
= *Asplenium paucijugum* F.Ballard
ST, P. Epiphyte or terrestrial in mountain forest, lowland forest or secondary forest at 50–1420 m.
- Athyrium* Roth (Woodsiaceae)
- ^R *Athyrium newtonii* (Baker) Diels
ST. In mountain forest, collected only at Pico at 1650 m, in the 19th century; it could be extinct in ST.
- Blechnum* L. (Blechnaceae)
- Blechnum attenuatum* (Sw.) Mett.
ST. Epiphyte or terrestrial in mountain forest at 800–1250 m.
- Blotiella* R.M.Tryon (Dennstaedtiaceae)
- Blotiella currorii* (Hook.) R.M.Tryon
= *Blotiella mannii* (Baker) Pic.Serm.
ST, P. Mountain forest at 1000–1400 m in ST and 500–650 m in P.
- Blotiella glabra* (Bory) R.M.Tryon
ST. Mountain forest at 1400–1900 m, collected once at low altitude.
- Bolbitis* Schott (Dryopteridaceae)
- Bolbitis acrostichoides* (Afzel. ex Sw.) Ching
ST, P. Mountain forest at 690–1100 m in ST, at lower altitude in P.
- Bolbitis auriculata* (Lam.) Alston
ST, P. Terrestrial in lowland forest at 150–800 m.
- Bolbitis fluviatilis* (Hook.) Ching
ST, P. Terrestrial in lowland forest and mountain forest at 200–1300 m.
- Christella* H.Lév. (Thelypteridaceae)
- Christella dentata* (Forssk.) Brownsey & Jermy
ST, P. Terrestrial in lowland forest at 200–760 m.

- Christella hispidula* (Decne.) Holttum
ST. Terrestrial in lowland forest and mountain forest at 100–1250 m.
- Coniogramme* Fée (Cryptogrammaceae)
- Coniogramme africana* Hieron.
ST. Terrestrial in mountain forest at 920–1800 m.
- Crepidomanes* (C.Presl) C.Presl (Hymenophyllaceae)
- Crepidomanes mannii* (Hook.) J.P.Roux
= *Trichomanes mannii* Hook.
ST. Epiphyte in mountain forest at 850–1000 m.
- Crepidomanes melanotrichum* (Schltdl.) J.P.Roux
= *Trichomanes pyxidiferum* var. *melanotrichum* (Schltdl.) Schelpe
ST. Mostly epiphyte in mountain forest at 900–1400 m.
- Ctenitis* (C.Chr.) C.Chr. (Dryopteridaceae)
- ^R *Ctenitis cirrhosa* (Schumach.) Ching
ST. Terrestrial or rarely epiphyte in mountain forest.
- Cyclosorus* Link (Thelypteridaceae)
- ^R *Cyclosorus striatus* (Schumach.) Ching
ST. Terrestrial fern collected only once in mountain forest.
- Davallia* Sm. (Davalliaceae)
- Davallia chaerophylloides* (Poir.) Steud.
ST. Mostly epiphyte in lowland forest at 200–600 m.
- Dicranopteris* Bernh. (Gleicheniaceae)
- Dicranopteris linearis* (Burm.f.) Underw.
ST. Mountain forest, lowland forest and secondary forest at 200–2020 m.
- Didymochlaena* Desv. (Dryopteridaceae)
- Didymochlaena truncatula* (Sw.) J.Sm.
ST. In mountain and lowland forests at 200–1430 m.
- Didymoglossum* Desv. (Hymenophyllaceae)
- Didymoglossum erosum* (Willd.) J.P.Roux
= *Trichomanes erosum* Willd.
ST, P. Epiphyte or terrestrial in forests at 80–1900 m.
- Diplazium* Sw. (Woodsiaceae)
- Diplazium nemorale* (Baker) Schelpe
= *Diplazium arborescens* var. *nemorale* (Baker) C.Chr.
ST. Mountain forest and lowland forest at 400–1400 m.
- Diplazium proliferum* (Lam.) Thouars
ST, P. Terrestrial in lowland forest, mountain forest and secondary forest up to 1200 m.
- Diplazium velaminosum* (Diels) Pic.Serm.
ST. In forest.
- Drynaria* (Bory) J.Sm. (Polypodiaceae)
- Drynaria laurentii* (H.Christ ex De Wild. & T.Durand) Hieron.
ST, P. Epiphyte in lowland forest at 50–760 m.

Drynaria volkensii Hieron.

ST, P. Epiphyte in lowland forest at 180–900 m.

Dryopteris Adans. (Dryopteridaceae)

^{R E} *Dryopteris caperata* J.P.Roux

ST. In forest.

^{R E} *Dryopteris cicatricata* J.P.Roux

ST. In mountain forest at c. 2000 m.

Dryopteris pentheri (Krasser) C.Chr.

ST. In mountain forest at 490–1850 m.

Elaphoglossum Schott ex J.Sm. (Dryopteridaceae)

Elaphoglossum acrostichoides (Hook. & Grev.) Schelpe

ST. Mountain forest at 1150–1900 m.

Elaphoglossum aubertii (Desv.) T.Moore

ST. Mountain forest at 1550–1900 m.

Elaphoglossum chevalieri H.Christ

ST, P. Epiphyte in mountain forest at 1500–1950 m in ST and 300–800 m in P.

Elaphoglossum isabelense Brause

ST, P. Epiphyte in mountain forest at 1000–1480 m in ST, unknown locality in P.

^R *Elaphoglossum lancifolium* (Desv.) C.V.Morton

= *Elaphoglossum salicifolium* (Willd. ex Kaulf.) Alston

ST. Collected only twice at low altitude and at Pico.

Grammitis Sw. (Polypodiaceae)

^R *Grammitis cryptophlebia* (Baker) Copel.

= *Grammitis molleri* (Baker) Schelpe

ST. Collected only once in mountain forest at 1900 m, in the 19th century; it could be extinct in ST.

^R *Grammitis ebenina* (Maxon) Tardieu

ST. Collected only once at 800 m, in the 19th century; it could be extinct in ST.

^{R E} *Grammitis nigrocincta* Alston

P. Collected only twice at 600 m, in 1956.

Histiopteris (J.Agardh) J.Sm. (Dennstaedtiaceae)

^R *Histiopteris incisa* (Thunb.) J.Sm.

ST, P. Mountain forest at 1000–1280 m in ST and c. 300 m in P; it could be extinct in ST and P.

Humata Cav. (Davalliaceae)

^R *Humata repens* (L.f.) Diels

ST. Collected only once in lowland forest, in the 19th century; it could be extinct in ST.

Huperzia Bernh. (Lycopodiaceae)

Huperzia dacrydioides (Baker) Pic.Serm.

= *Huperzia mildbraedii* (Herter) Pic.Serm.

ST, P. Epiphyte in mountain forest at 1000–1900 m in ST and 200–900 m in P.

Huperzia ophioglossoides (Lam.) Rothm.

ST. Epiphyte in mountain forest at 1850–2020 m.

Huperzia phlegmaria (L.) Rothm.

ST, P. Epiphyte in lowland forest and mountain forest at 100–2000 m.

Huperzia verticillata (L.f.) Trevis.

ST. Epiphyte in mountain forest at 1100–1400 m.

Huperzia warneckei (Herter ex Nessel) Pic.Serm.

ST. Epiphyte in lowland forest and mountain forest at 170–1100 m.

Hymenophyllum Sm. (Hymenophyllaceae)

Hymenophyllum capillare Desv. var. *alternialatum* (Pic.

Serm.) Faden

ST. Epiphyte or terrestrial in mountain forest at 1225–2000 m.

^R *Hymenophyllum digitatum* (Sw.) Fosberg

= *Trichomanes digitatum* Sw.

ST. Collected only once at 1400 m, in 1956.

Hymenophyllum hirsutum (L.) Sw.

ST. Epiphyte or rarely terrestrial in mountain forest at 900–2000 m.

Hymenophyllum kuhnii C.Chr.

= *Hymenophyllum polyanthos* var. *kuhnii* (C.Chr.)

Schelpe

= *Hymenophyllum polyanthos* var. *mildbraedii* (Brause ex Brause & Hieron.) Schelpe

ST, P. Epiphyte in mountain forest at 800–1950 m in ST and 500–600 m in P.

Hymenophyllum splendidum Bosch

ST, P. Terrestrial or epiphyte in mountain forest at 1000 m in ST and 600 m in P.

Hypolepis Bernh. (Dennstaedtiaceae)

Hypolepis sparsisora (Schrader) Kuhn

ST. Terrestrial in mountain forest at 1000–1250 m.

Lastreopsis Ching (Dryopteridaceae)

^R *Lastreopsis* aff. *curreri* (Mett. ex Kuhn) Tindale

P. In forest, a rare fern collected only twice [*Navel* 138 (LISU); *Rozeira* 2607 (PO)].

Lellingeria A.R.Sm. & R.C.Moran (Polypodiaceae)

^R *Lellingeria oosora* (Baker) A.R.Sm. & R.C.Moran

= *Xiphopteris oosora* (Baker) Alston

ST. Collected only once in mountain forest at 1950 m; it could be extinct in ST.

^{R E} *Lellingeria tomensis* (Schelpe) Parris

= *Grammitis tomensis* Schelpe

ST. Collected only twice in mountain forest at 2000 m, in the 19th century; it could be extinct.

Lepisorus (J.Sm.) Ching (Polypodiaceae)

Lepisorus excavatus (Bory ex Willd.) Ching

= *Pleopeltis excavata* (Bory ex Willd.) Sledge

ST. Terrestrial or epiphyte in mountain forest at 800–2000 m.

Lepisorus spicatus (L.f.) Li Wang

= *Belvisia spicata* (L.f.) Mirb. ex Copel.

ST. Terrestrial or epiphyte in lowland forest and secondary forest at 140–1100 m.

Lomariopsis Fée (Lomariopsidaceae)

Lomariopsis guineensis (Underw.) Alston

ST, P. Lowland forest at 100–700 m.

Lomariopsis hederacea Alston

ST, P. Mountain forest at 290–1300 m in ST and 500–800 m in P.

^R *Lomariopsis warneckei* (Hieron.) Alston

P. Epiphyte in forest.

Loxogramme (Blume) C.Presl (Polypodiaceae)

Loxogramme abyssinica (Baker) M.G.Price

= *Loxogramme lanceolata* auct. non C.Presl

ST, P. Mostly epiphyte in lowland forest and mountain forest at 300–1800 m.

Lonchitis L. (Lindsaeaceae)

^R *Lonchitis occidentalis* Baker

ST. Collected only in two localities at 200 and 1290 m; it could be extinct in ST.

Lycopodiella Holub (Lycopodiaceae)

Lycopodiella cernua (L.) Pic.Serm.

ST, P. Lowland forest and mountain forest at 100–2000 m.

Lycopodium L. (Lycopodiaceae)

^R *Lycopodium clavatum* L.

ST. Mountain forest at 1850–2000 m.

Megalastrum Holttum (Dryopteridaceae)

^R *Megalastrum lanuginosum* (Willd. ex Kaulf.) Holttum

= *Ctenitis lanuginosa* (Willd. ex Kaulf.) Copel.

ST. Locality unknown. A rare fern elsewhere, occurring mostly above 1000 m; it could be extinct in ST.

Metathelypteris (H.Ito) Ching (Thelypteridaceae)

^R *Metathelypteris fragilis* (Baker) Holttum subsp.

guineensis Benl

ST. In mountain forest at 1000–1200 m.

Microgramma C.Presl (Polypodiaceae)

Microgramma mauritiana (Willd.) Tardieu

= *Anapeltis lycopodioides* (L.) J.Sm. var. *owariensis* (Desv.) Benl

ST, P. Mostly epiphyte in lowland forest, secondary forest and plantations up to 900 m, but collected once at Pico.

Microlepia C.Presl (Dennstaedtiaceae)

^R *Microlepia speluncae* (L.) T.Moore

ST. Collected at 760 m and under 110 m; it could be extinct in ST.

Microsorium Link (Polypodiaceae)

Microsorium punctatum (L.) Copel.

ST, P. Terrestrial or epiphyte in lowland forest or mountain forest up to 1200 m.

Microsorium scolopendria (Burm.f.) Copel.

= *Phymatosorus scolopendria* (Burm.f.) Pic.Serm.

ST, P. Terrestrial or epiphyte, common in lowland forest, secondary forest and plantations up to 850 m, and collected once at 1000 m.

Nephrolepis Schott (Nephrolepidaceae)

Nephrolepis biserrata (Sw.) Schott

ST, P. Terrestrial or epiphyte, very abundant in lowland forest and mountain forest at 50–1300 m.

Nephrolepis cordifolia (L.) C.Presl var. *pumicicola*

(F.Ballard) Hovenkamp & Miyam.

= *Nephrolepis pumicicola* F.Ballard

ST. Terrestrial or epiphyte, on lava and in rock fissures in mountain forest at 1380–1500 m; abundant in crater Lagoa Amélia.

Nephrolepis undulata (Afzel. ex Sw.) J.Sm.

ST, P. Terrestrial or epiphyte in lowland forest and mountain forest at 100–2020 m.

Odontosoria (C.Presl) Fée (Lindsaeaceae)

^R *Odontosoria afra* (K.U.Kramer) J.P.Roux

= *Odontosoria chinensis* var. *divaricata* auct. non H.Christ

ST. Terrestrial in mountain forest at 1500–1900 m.

Oleandra Cav. (Oleandraceae)

Oleandra distenta Kunze

ST, P. Mostly epiphyte in mountain forest at 950–1250 m, collected once at low altitude.

Ophioglossum L. (Ophioglossaceae)

Ophioglossum costatum R.Br.

ST. Terrestrial, rare, in mountain forest at 900–1200 m.

Ophioglossum reticulatum L.

ST. Lowland forest and mountain forest at 50–1200 m.

Pellaea Link (Sinopteridaceae)

Pellaea doniana J.Sm. ex Hook.

ST, P. Lowland forest up to 600 m in ST and 300–350 m in P.

Pityrogramma Link (Pteridaceae)

**Pityrogramma calomelanos* (L.) Link var. *calomelanos*

ST, P. Terrestrial in secondary forest, in plantations and on roadsides.

Platycerium Desv. (Polypodiaceae)

Platycerium stemaria (P.Beauv.) Desv.

ST, P. Mostly epiphyte in lowland forest and secondary forest up to 380 m.

Pleopeltis Humb. & Bonpl. ex Willd. (Polypodiaceae)

^R *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf.

ST. Epiphyte in mountain forest at c. 1400 m.

Pneumatopteris Nakai (Thelypteridaceae)

Pneumatopteris afra (H.Christ) Holttum

ST, P. Terrestrial in lowland forest, secondary forest, plantations and mountain forest at 50–1400 m.

Pneumatopteris oppositifolia (Hook.) Holttum

ST. Terrestrial in lowland forest and mountain forest at 50–1800 m.

Pneumatopteris venulosa (Kuntze) Holttum

ST, P. Terrestrial in lowland forest and mountain forest at 200–1400 m.

Polyphlebium Copel. (Hymenophyllaceae)

^R *Polyphlebium borbonicum* (Bosch) Ebihara & Dubuisson
= *Trichomanes borbonicum* Bosch

ST. Epiphyte in mountain forest at 1200–2000 m; it could be extinct in ST.

Pseudophegopteris Ching (Thelypteridaceae)

^{R E} *Pseudophegopteris henriquesii* (Baker) Holttum

ST. Mountain forest at 750–1250 m.

Psilotum Sw. (Psilotaceae)

^R *Psilotum nudum* (L.) P.Beauv.

ST. Terrestrial or epiphyte, known from a single locality at c. 100 m, collected in 1954.

Pteridium Gled. ex Scop. (Dennstaedtiaceae)

Pteridium aquilinum (L.) Kuhn subsp. *capense* (Thunb.) C.Chr.

ST, P. In mountain forest and secondary forest at 760–1900 m.

Pteris L. (Pteridaceae)

Pteris atrovirens Willd. forma *atrovirens*

ST, P. Lowland forest, secondary forest and mountain forest at (20–) 100–1800 m.

^R *Pteris burtonii* Baker

P. Unknown locality; it could be extinct in ST.

Pteris dentata Forssk.

= *Pteris dentata* subsp. *flabellata* (Thunb.) Runemark
ST, P. Mountain forest at c. 1400 m in ST and 600 m in P.

Pteris linearis Poir.

ST, P. Lowland forest at 200–900 m, collected once at 1400 m in ST.

^R *Pteris muricella* Fée

Pteris pteridioides (Hook.) F.Ballard
ST. Mountain forest at 1200–1300 m.

Pteris similis Kuhn

ST, P. Lowland forest at 10–760 m.

Pteris togoensis Hieron.

Pteris paucipinnata Alston
ST, P. Lowland forest and mountain forest at 350–1800 m.

^R *Pteris tripartita* Sw.

ST, P. Lowland forest up to 200 m; it has not been collected since 1905.

**Pteris vittata* L.

ST. At 100–700 m.

Ptisana Murdock (Marattiaceae)

Ptisana fraxinea (Sm.) Murdock

= *Marattia fraxinea* Sm.

ST, P. Terrestrial, frequent in primary and secondary forest at 10–1400 m.

Pyrrosia Mirb. (Polypodiaceae)

^R *Pyrrosia lanceolata* (L.) Farw.

ST, P. Epiphyte in lowland forest up to 300 m.

Selaginella P.Beauv. (Selaginellaceae)

Selaginella cathedriformis Spring

P. Lowland forest at 300–650 m.

^E *Selaginella mannii* Baker

ST, P. Terrestrial in mountain forest at 900–1900 m in ST and c. 600 m in P.

Selaginella molleri Hieron.

ST. Lowland forest and mountain forest at 490–1250 m.

Selaginella molliceps Spring

ST, P. Lowland forest, mountain forest and secondary forest at 20–1250 m in ST and 100–900 m in P.

^{R E} *Selaginella monodii* Alston

ST. Known only from two localities, at 80 m and 600 m.

^R *Selaginella myosurus* (Sw.) Alston

P. Unknown locality; it could be extinct in P.

^R *Selaginella squarrosa* Baker

P. Collected only once at 500–600 m.

Selaginella thomensis Alston

ST. Mountain forest at 890–1950 m.

Sphaerostephanos J.Sm. ex Hook. (Thelypteridaceae)

^{R E} *Sphaerostephanos elatus* (Bojer) Holttum subsp. *thomensis* Holttum

ST. In forest.

Tectaria Cav. (Tectariaceae)

Tectaria angelicifolia (Schumach.) Copel.

ST, P. Lowland forest at 200–550 m.

Tectaria camerooniana (Hook.) Alston

ST. Mountain forest at 690–1420 m.

Tectaria fernandensis (Baker) C.Chr.

ST, P. Mountain forest and lowland secondary forest at 20–1800 m.

Terpsichore A.R.Sm. (Polypodiaceae)

Terpsichore cultrata (Bory ex Willd.) A.R.Sm.

Xiphopteris cultrata (Willd.) Schelpe

ST. Rare epiphyte in mountain forest at 800–1420 m.

Trichomanes L. (Hymenophyllaceae)

Trichomanes crispiforme Alston

ST, P. Epiphyte in forest and secondary forest at 300–800 m in P and collected only once in ST.

Triplophyllum Holttum (Tectariaceae)***Triplophyllum buchholzii*** (Kuhn) Holttum

P. Mountain forest and lowland forest at 60–800 m.

^{R E} ***Triplophyllum fraternum*** (Mett. ex Kuhn) Holttum var. ***elongatum*** (Hook.) Holttum

P. In forest, collected once in the 19th century; it could be extinct.

Triplophyllum heudelotii Pic.Serm.

ST, P. In forest.

^R ***Triplophyllum jenseniae*** (C.Chr.) Holttum

P. Collected only once in forest at 850 m.

Triplophyllum principis Holttum

P. Lowland forest at 60–600 m.

Triplophyllum protensum (Afzel. ex Sw.) Holttum

ST, P. Lowland forest at 20–900 m in ST and 200–600 m in P.

Triplophyllum securidiforme (Hook.) Holttum var. ***securidiforme***

ST, P. Mountain forest and lowland forest at 60–1200 m.

Triplophyllum vogelii (Hook.) Holttum

ST. Collected once in lowland forest at c. 500 m.

Vandenboschia Copel. (Hymenophyllaceae)***Vandenboschia radicans*** (Sw.) Copel.

= *Trichomanes radicans* Sw.

ST. Epiphyte or terrestrial in forest at 20–1800 m.

Vittaria Sm. (Adiantaceae)***Vittaria guineensis*** Desv. var. ***orientalis*** Hieron.

ST, P. Epiphyte in lowland forest, secondary forest and mountain forest at 80–1800 m.

Vittaria owariensis Fée

ST, P. Epiphyte in lowland forest at 100–200 m, collected once above 1000 m.

Zygophlebia L.E.Bishop (Polypodiaceae)^R ***Zygophlebia villosissima*** (Hook.) L.E.Bishop

= *Xiphopteris villosissima* (Hook.) Alston

ST. In forest at 1400 m.

ACKNOWLEDGEMENTS

We thank Prof. Gideon F. Smith of the South African National Biodiversity Institute for support, and two anonymous referees for suggesting improvements to the manuscript.

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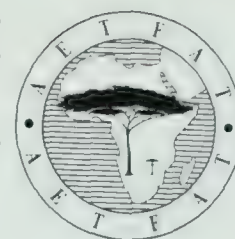
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Manuscript received 23 Sep. 2010; accepted in revised version 14 Mar. 2011.

Communicating Editor: Thomas Janssen.



Alien and indigenous plant species diversity of homegardens of a rural settlement in the eastern Kalahari, South Africa

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Background and aims – The green infrastructure of rural settlements is represented by various land-uses which are of potential importance for the maintenance of biodiversity. Especially homegardens play an important part, but regardless of the knowledge that is available on the floras of urban environments, this feature has never been specifically quantified for South Africa, or any other southern Africa country. The aim of this study is to describe the contribution of homegardens towards the urban green infrastructure of a rural settlement in South Africa in terms of plant diversity and to provide a baseline for future research on urban floras of larger or culturally different urban areas.

Methods – A grid provided 118 suitable sampling points for 20 × 20 m sample plots. Each sample plot consisted of five transects of twenty points each. At each of the 100 points the closest tree, shrub, forb and grass was recorded within a 0.5 m radius. For the purposes of this descriptive study, the frequency data was converted to presence-absence data.

Key results – The four land-use types of Tlhakgameng is habitat for 460 species, in 302 genera and 96 plant families. Of these species 56% are alien to Tlhakgameng. The two most dominant families were the Asteraceae and Poaceae and the most dominant genera *Acacia* and *Eragrostis*. The five most dominant species for the study area were all indigenous. A total of 27 South African endemic and eight Red List species were recorded from the settlement. Homegardens had the highest gamma diversity which was mainly alien species cultivated for their uses. Food plants and ornamentals made up the majority (68%) of the garden flora. Most of the alien species originate from Asia and the Americas, some of which are counted with the 41 declared invaders and weeds recorded from the study area.

Conclusion – This study confirms that rural settlements, like urban environments, are floristically diverse. The results of this study revealed that homegardens have the highest species richness as compared to other types of land-use in a rural settlement. The majority of the species found in homegardens were cultivated horticultural floras, and indigenous and alien weeds. Homegardens also provide a refuge for endemic or threatened species. The various needs of households in Tlhakgameng seem to sustain the growth of a rich and diverse mixture of multipurpose species in homegardens.

Key words– Asteraceae, biodiversity, *Cynodon dactylon*, ethnobotany, invasive aliens, land-use, savanna.

INTRODUCTION

A large proportion of green infrastructure in urban areas is represented by domestic gardens which are of potential importance for the maintenance of biodiversity in such areas (Smith et al. 2005, Thompson et al. 2005, Smith et al. 2006). However, ecological studies on domestic gardens are quite rare, probably due to problems with multiple ownership, the extremely dynamic nature of the gardens, and as they are unregulated habitats with no recommended planning and management criteria or restrictions (Gaston et al. 2005, Mathieu

et al. 2007). From a scientific point of view, the biodiversity value of domestic gardens is also questioned as they appear to be too small to be biologically significant (Thompson et al. 2003, Gaston et al. 2005, Mathieu et al. 2007). Ironically, as a composite the total area of domestic gardens is too large to be ignored as they represent quite a substantial part of the vegetated area in most cities. Domestic gardens cover up to 26% of the urban area of cities in the United Kingdom (Gaston et al. 2005, Loram et al. 2007) and 36% of the urban area in Dunedin, New Zealand (Mathieu et al. 2007).

According to Gaston et al. (2005), domestic gardens offer a great opportunity to increase biodiversity and maintain the provision of ecosystem services in urban areas. It was further indicated by Loram et al. (2007) that the greater the degree of urbanisation the more important gardens become as a biodiversity resource. Although private gardens are quite small, they differ from most other urban green spaces which are notoriously patchy, in that they are inter-connected (Smith et al. 2005) and link green areas inside the harsh artificial urban environment with each other (Mathieu et al. 2007). Domestic gardens are identified by Gaston et al. (2005) as private spaces adjacent to or surrounding dwellings, comprising of lawns, ornamental and vegetable plots, trees, ponds, paths, patios and temporary buildings, which are quite similar all over the world but variable in terms of form and uses. At this point it is required to define homegardens, the focus of this study, which is a type of domestic garden. Homegardens are defined as intensively worked, land-use systems involving deliberate management of multipurpose plants in association with agricultural crops, and invariably livestock, within the compounds of individual households (Fernandes & Nair 1986). In rural homegardens, gardeners usually grow fruit, vegetables, medicinal, spiritual and ornamental plants (Lamont et al. 1999, Kumar & Nair 2004).

Most existing biodiversity studies of domestic gardens occurred in developed countries with the main objective to describe the size and composition of gardens as a resource for biodiversity (Thompson et al. 2005, Smith et al. 2006) and ecosystem functioning (Gaston et al. 2005). Results of these studies are relevant to all temperate gardens in the northern hemisphere (Thompson et al. 2003) and have shown that gardens provide a complex and heterogeneous mosaic of habitats which have unique ecological features that support quite a diversity of plants and animals. In developing countries, the emphasis of homegarden studies are more on

horticulture, urban agriculture and agroforestry, and include rural areas (Rugalema et al. 1994, High & Shackleton 2000, Winklerprins 2002, Pandey et al. 2007). The major contributor to the diversity of urban environments is horticultural floras which are mostly characterized by ornamental plants and vegetables (Gaston et al. 2005, Marco et al. 2008). Plant diversity in homegardens is regarded as important in terms of providing subsistence and income to the households (May & Rogerson 1995, Das & Das 2005, Pandey et al. 2007), while they are regarded as extremely important in maintaining a sense of aesthetic pride, as well as a template for knowledge transfer (Winklerprins 2002, Kumar & Nair 2004, Zobolo & Mkabela 2006).

Regardless of the knowledge that is available on the floras of urban environments, this feature has never been specifically quantified for South Africa, or any other southern Africa country. This study is a follow-up to the work of Molebatsi et al. (2010) which defined the traditional Tswana *tshimo* (homegarden) and Lubbe et al. (2010) that quantified the flora of an urban environment where Tswana and western cultures meet. The aim of this study is to describe the contribution of homegardens towards the urban green infrastructure of a rural settlement in terms of plant diversity and to provide a baseline for future research on urban floras of larger or culturally different urban areas. The objectives were to (i) assess the most abundant taxa, (ii) calculate the frequency of occurrence of threatened, endemic and invasive species, (iii) compare the dominant growth forms, (iv) determine the origin of alien cultivated and naturalized species, and (v) document the useful plant diversity of the study area. Additionally, a comparison of the garden flora with that of other land-use types in the settlement is made to determine the contribution that homegardens make towards the total plant diversity of the study area.

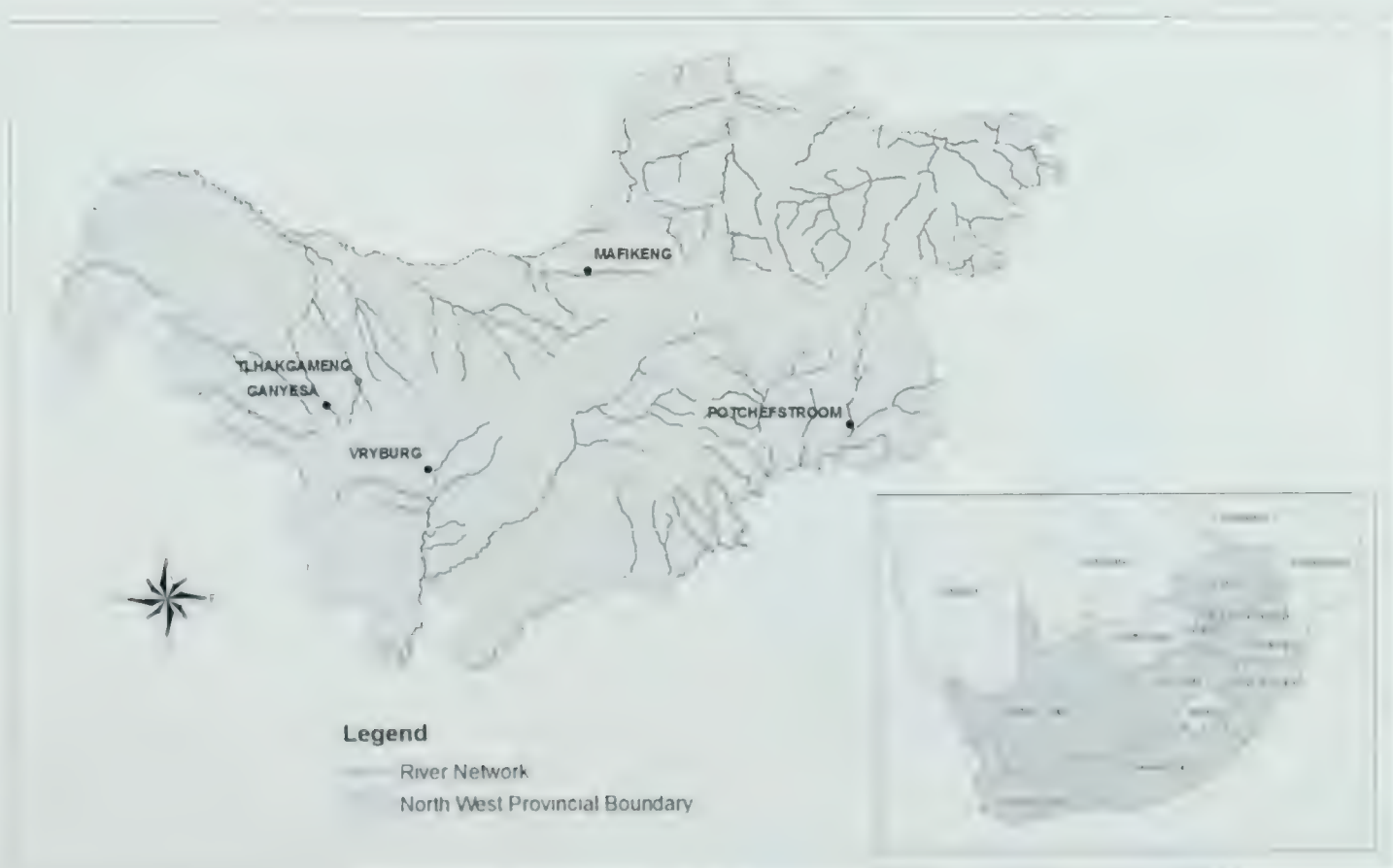


Figure 1 – Location of Tlhakgameng in the North-West Province and other main settlements of the province.

MATERIALS AND METHODS

Study area

The study was conducted in the deep rural setting of Tlhakgameng in the North-West Province of South Africa (fig. 1). It is situated 150 km west of the provincial capital, Mafikeng, and 80 km south of the Botswana border. We defined deep rural as an inhabited area where a tribal authority manages the community and 90% of the inhabitants are subsistence farmers.

The Tlhakgameng settlement lies in the eastern Kalahari and has a homogeneous landscape, with an altitude ranging between 1100 and 1400 m above sea level. The region is characterized by flat or gently undulating plains of Aeolian Kalahari sands of tertiary to recent origin. The vegetation is classified as Mafikeng Bushveld (Mucina & Rutherford 2006).

The Mafikeng Bushveld vegetation unit is characterized by summer rainfall with very dry winters (Mucina & Rutherford 2006). The annual rainfall varies from 350 to 520 mm. During the winter months frost is a frequent phenomenon. Rainfall patterns are erratic, for instance in 2006 the Tlhakgameng region experienced an above average rainfall year of 730 mm, while in 2007 the mean annual rainfall dropped to 267 mm (ARC-ISCW 2009). Temperatures for Tlhakgameng varies between -1.8°C and 36°C, with a mean annual temperature of 17.5°C. The mean daily maximum temperature is 27°C, while the mean daily minimum temperature is 9°C (ARC-ISCW 2009).

Sampling, data collection and analysis

Geographic Information System (GIS) techniques (ESRI 2006) were applied to overlay a grid on the Tlhakgameng region with gridpoints 500 m apart. A grid with a total of 118 gridpoints was generated to cover the four major land-use types of the study area (translating into 51 sample points in residential areas, 34 in natural areas, 17 in drainage lines and 16 in fallow fields). For the purpose of the plant survey, a plot of 20 × 20 m with five transects of twenty points each were placed at each gridpoint. At each point the closest tree, shrub, forb (non-grassy herbaceous plant) and grass was noted. To determine and analyse the floristic composition of Tlhakgameng, only presence-absence data was sourced from the frequency tables. Frequency data was analysed and applied in a different study to evaluate plant diversity patterns along a socio-economic gradient (Molebatsi 2010).

Indigenous and alien species data was categorized according to conservation status (Raimondo et al. 2009), life and growth form, and geographical distribution (Germishuizen et al. 2006) for analyses. Indigenous and alien species were artificially classified into categories as useful (ornamental, vegetable, fruit, medicinal and hedge) or weeds (ruderals) based on several publications (Bromilow 2001, Van Wyk et al. 1997, Pienaar 2000, Van Wyk & Gericke 2000, Glen 2002, Van Wyk 2005). In terms of invasive aliens the declared weeds and invaders covered by the Conservation of Agricultural Resources Act (Act 43 of the Republic of South Africa 1983) were also identified. Declared weeds (category 1) are prohibited in South Africa and must be controlled,

declared invaders (category 2) are allowed in demarcated areas under controlled conditions and declared invaders (category 3) must not be planted or traded (Henderson 2001). For the purpose of this paper, the following definitions were used with regard to species classification as indigenous or alien:

- Indigenous – naturally occurring within the study area, usually not cultivated.
- Indigenous cultivated – indigenous to South Africa and not occurring naturally within the study area, but cultivated in gardens.
- Naturalised – not indigenous to South Africa, but occurs in the study area where it sustains self-replacing populations outside of cultivation without direct intervention by people (includes invasive aliens).
- Alien cultivated – not indigenous to South Africa and not naturalised in the study area, but cultivated in gardens and including garden hybrid species (includes invasive aliens).

Voucher specimens were identified and deposited in the AP Goossens Herbarium (PUC) and duplicate specimens in the Pretoria National Herbarium (PRE) for verification.

RESULTS

Largest families

A total of 96 plant families were recorded for all land-use types in Tlhakgameng, representing 460 species. The ten most dominant families represent 219 species (48%) of the total number of species recorded (table 1). Families with the highest number of taxa were the Asteraceae, Fabaceae and Poaceae which are also amongst the top ten largest families in South Africa (Germishuizen et al. 2006).

Largest genera

In total, 302 genera were recorded for all land-use types in Tlhakgameng. The ten largest genera represent 11% of the total number of recorded species for all land-use types (table 2). Six of the ten largest genera belong to five of the most dominant families found in Tlhakgameng. The Poaceae and

Table 1 – The ten most dominant plant families for Tlhakgameng based on the number of species per family.

Four families are also ranked as part of the top ten for South Africa and are indicated with their position in superscript.

Rank	Family	Species
1.	Asteraceae ¹	59
2.	Fabaceae ²	43
3.	Poaceae ⁷	41
4.	Solanaceae	14
5.	Crassulaceae	12
6.	Lamiaceae	11
7.	Cactaceae	10
	Malvaceae	10
	Mesembryanthemaceae ³	10
10.	Amaranthaceae	9

Table 2 –The ten most dominant genera for Tlhakgameng based on the number of species per genus.

Rank	Genus	Family	Spp.
1.	<i>Eragrostis</i>	Poaceae	9
2.	<i>Acacia</i>	Fabaceae	8
3.	<i>Aloe</i>	Asphodelaceae	5
	<i>Indigofera</i>	Fabaceae	5
	<i>Ipomoea</i>	Convolvulaceae	5
	<i>Solanum</i>	Solanaceae	5
7.	<i>Amaranthus</i>	Amaranthaceae	4
	<i>Aristida</i>	Poaceae	4
	<i>Asparagus</i>	Asparagaceae	4
	<i>Euphorbia</i>	Euphorbiaceae	4

Fabaceae are each represented by two of the largest genera in the study area, the grass genera *Eragrostis* and *Aristida* and legume genera *Acacia* and *Indigofera* (table 2). Six of the 53 species belonging to the ten most dominant genera of Tlhakgameng are alien to South Africa, but these taxa were not excluded from the calculations as all the genera are indigenous.

Dominant species

The twenty plant species that were recorded most frequently (electronic appendix 1) were all present in more than half of the land-use types. *Cynodon dactylon* was ranked as the most frequently recorded species as it occurred in 86% of sample plots. It also occurs frequently in sample plots. Another grass species, *Eragrostis lehmanniana*, had the second highest frequency (75%). The three remaining species in the top five were the shrub *Acacia hebeclada* (75%), geophyte *Bulbine abyssinica* (72%) and forb *Felicia muricata* (69%). Three of the twenty most abundant species in Tlhakgameng are naturalized aliens in South Africa, compared to two indigenous cultivated species and 15 naturally occurring indigenous species (electronic appendix 1). More than half of the twenty most abundant species belong to three families, namely the Poaceae (six species), Asteraceae and Fabaceae (both three species).

Endemic species

A total of 27 species which are endemic to South Africa were recorded in Tlhakgameng (electronic appendix 2). The majority of these species were commonly cultivated except for five naturally occurring species, namely *Crabbea angustifolia*, *Eragrostis pseud-obtusa*, *Hypertelis arenicola*, *Selago mixta* and *Sida spinosa*. *Carpobrotus edulis* occurred most frequently in 12% of sampled plots, *Sida spinosa* in 10%, and *Selago mixta* was represented by the highest number of individuals amongst all, but only occurred in 9% of the sample plots (electronic appendix 2). *Aptenia cordifolia* and *Tulbaghia violacea*, two cultivated indigenous species, had the highest numbers of individuals, but both only occurred in 4% of the sampled plots, mainly in homegardens. The Mesembryanthemaceae was represented by six species in the endemic list.

Threatened species

According to the South African Red Data List of plants (Raimondo et al. 2009), eight species recorded for Tlhakgameng have a threat status; including species listed as declining (5), near threatened (2) and vulnerable (1). The most common of these was *Drimia sanguinea* (near threatened) occurring in all land-use types (44% of sample plots), while *Acacia erioloba* (declining) occurred in 26% and *Cotyledon orbiculata* (near threatened) in 16%. The occurrence of all the remaining species was less than 10% for all sampled plots (electronic appendix 3). Half of these species are cultivated in homegardens and the rest occur naturally.

Useful cultivated flora

The majority of species cultivated in homegardens in Tlhakgameng were ornamentals (fig. 2). Most frequently occurring species in each plant use category include the trees *Prunus persica* (food) and *Schinus molle* (shade), the shrubs *Dodonaea viscosa* (hedge) and *Nerium oleander* (ornamental), and forb *Schkuhria pinnata* (medicinal) (table 3). Eight of the most cultivated useful plants were alien species. Food plants and medicinal plants dominate the list. The most dominant species are all indigenous and naturally occurring.

Origin of alien species

The largest portion of the species found in all land-use types of the study area is not indigenous to Tlhakgameng (56% of the species). This large proportion includes 32% alien cultivated, 13% indigenous cultivated and 11% naturalized species (Germishuizen et al. 2006). From the 51 sample plots of homegardens, the majority of alien cultivated species (21%) were found to originate from Asia, but only 4% of naturalized species (electronic appendix 4). The second highest contributor was South America with 15% of alien cultivated species and 41% of naturalized species. Central and North America followed, both with 13% of alien cultivated species and with 21% and 11% of naturalized species respectively. All the remaining regions of origin were found to contribute

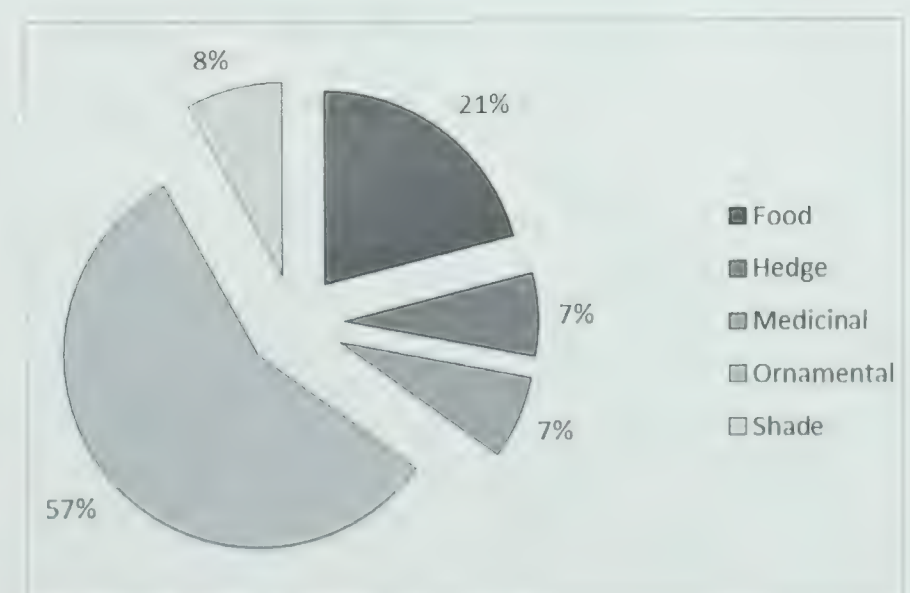


Figure 2 – Proportion of the total useful plant flora contributing to each plant use category for both alien and indigenous species in homegardens of Tlhakgameng.

Table 3 – The twenty most-frequently occurring useful plants in homegardens of Tlhakgameng.
F, the percentage of homegarden sample plots (n=51) in which the species was recorded; D, mean number of individuals per set of recorded plots.

Species name	Growth form	Family	Use	F	Plots	D
<i>Schkuhria pinnata*</i>	Forb	Asteraceae	Medicinal	78	40	8
<i>Sida cordifolia</i>	Forb	Malvaceae	Medicinal	75	38	4
<i>Felicia muricata</i>	Forb	Asteraceae	Medicinal	73	37	22
<i>Prunus persica*</i>	Tree	Rosaceae	Food	71	36	3
<i>Bulbine abyssinica</i>	Succulent	Asphodelaceae	Medicinal	69	35	18
<i>Portulaca oleracea*</i>	Succulent	Portulacaceae	Food	65	33	4
<i>Mollugo cerviana</i>	Forb	Molluginaceae	Medicinal	65	33	3
<i>Dodonaea viscosa</i>	Tree	Sapindaceae	Hedge	65	33	8
<i>Pollichia campestris</i>	Forb	Caryophyllaceae	Food fruit	61	31	5
<i>Acacia hebeclada</i>	Shrub	Fabaceae	Medicinal	61	31	29
<i>Morus alba*</i>	Tree	Moraceae	Food	59	30	1
<i>Senna italica</i>	Herb	Fabaceae	Medicinal	59	30	12
<i>Ziziphus mucronata</i>	Tree	Rhamnaceae	Medicinal	57	29	2
<i>Ficus carica*</i>	Shrub	Moraceae	Food	51	26	1
<i>Schinus molle*</i>	Tree	Anacardiaceae	Shade	49	25	1
<i>Zea mays*</i>	Graminoid	Poaceae	Food	47	24	11
<i>Nerium oleander*</i>	Shrub	Apocynaceae	Ornamental	47	24	2
<i>Citrillus lanatus</i>	Forb	Cucurbitaceae	Food	45	23	4
<i>Acrotome inflata</i>	Forb	Lamiaceae	Medicinal	45	23	2
<i>Acacia tortilis</i>	Tree	Fabaceae	Shade	45	23	2

less than 10% towards alien cultivated and naturalised species (electronic appendix 4).

Invasive species

In all land-use types sampled, 41 declared invader and weed species were found (Henderson 2001). Category 1 declared weeds had the highest number of species (22) and included, amongst others, *Nerium oleander* which occurred in 20% of the sampled plots. This was followed by Category 3 declared invaders (10 species) such as *Morus alba* (59% of the homegarden sample plots) and Category 2 declared invaders (8 species) such as *Prosopis glandulosa* (39% of the homegarden sample plots) (table 4).

Growth forms

The most abundant growth form found within all the land-use types were the forbs, with homegardens ranking the highest as compared to other land-use type with 168 forb species (37%), followed by natural areas with 78 (17%), wetlands with 64 (14%) and fallow fields with 36 (8%) species (electronic appendix 5). Dominant forb species found for all land-use types were *Felicia muricata* occurring in 69% of the sampled plots, while *Senna italica* occurred in 65% of the sampled plots. The second most abundant growth form was shrubs, where homegardens also ranked high in comparison with other land-use types with 82 species (18%), natural areas with 35 (8%), wetlands with 25 (5%) and fallow fields with 15 species (3%). Dominant shrub species for all

land-use types were *Acacia hebeclada* occurring in 75% and *Tarchonanthus camphoranthus* in 36% of the sampled plots.

The third most abundant growth form was trees, with homegardens having 60 species (13%), natural areas with 18 species (4%), wetlands with 14 species (3%) and fallow fields with 5 species (1%). Dominant tree species found for all land-use types were *Prunus persica* occurring in 31% of sample plots. The remaining growth forms (succulents, graminoids, geophytes and climbers) were also best represented in homegardens. Dominant species for these growth forms were as follows: succulents – *Portulaca quadrifida* and *Portulaca oleracea*; graminoids – *Cynodon dactylon* and *Schmidtia pappaphoroides*; geophytes – *Bulbine abyssinica* and *Harpagophytum procumbens*; climbers – *Citrillus lanatus* and *Vitis vinifera*.

Total species diversity

The 460 plants species of Tlhakgameng is made up of 201 indigenous (44%), 146 alien cultivated (32%), 60 indigenous cultivated (13%) and 53 naturalized (11%) species (fig. 3). In comparison to other land-use types, homegardens have the richest species diversity of alien, indigenous cultivated and naturalized species (fig. 4). However, natural areas have the highest number of indigenous species in comparison to other land-use types. In homegardens, alien cultivated species were found to be the most dominant as compared to other categories. Naturalized species found in homegardens were low compared to indigenous cultivated ones, but still the highest for the study area (fig. 4). The dominant species recorded for the homegardens were *Zea mays* and *Prunus persica* (alien

Table 4 – Declared alien invaders recorded from homegardens in Tlhakgameng.
F, the percentage of homegarden sample plots (n=51) in which the species was recorded; D, mean number of individuals per set of recorded plots; C (Henderson 2001), Category 2 – declared invader, Category 3 – declared invader and cultivation thereof prohibited.

Species name	Growth form	Family	C	F	Plots	D
<i>Morus alba</i>	Tree	Moraceae	3	59	30	1
<i>Schinus molle</i>	Tree	Anacardiaceae	3	49	25	1
<i>Prosopis glandulosa</i>	Tree	Fabaceae	2	39	20	1
<i>Melia azedarach</i>	Tree	Meliaceae	3	35	18	1
<i>Casuarina cunninghamiana</i>	Tree	Casuarinaceae	2	22	11	2
<i>Mirabilis jalapa</i>	Forb	Nyctaginaceae	3	22	11	1
<i>Ailanthus altissima</i>	Tree	Simaroubaceae	3	16	8	1
<i>Atriplex nummularia</i>	Shrub	Chenopodiaceae	2	10	5	4
<i>Gleditsia triacanthos</i>	Tree	Fabaceae	2	6	3	1
<i>Ipomoea purpurea</i>	Climber	Convolvulaceae	3	4	2	1
<i>Jacaranda mimosifolia</i>	Tree	Bignoniaceae	3	4	2	1
<i>Robinia pseudoacacia</i>	Tree	Fabaceae	2	4	2	2
<i>Acacia decurrens</i>	Tree	Fabaceae	2	2	1	1
<i>Berberis thunbergii</i>	Shrub	Berberidaceae	3	2	1	1
<i>Grevillea robusta</i>	Tree	Proteaceae	3	2	1	1
<i>Leucaena leucocephala</i>	Tree	Fabaceae	2	2	1	1
<i>Ligustrum lucidum</i>	Tree	Oleaceae	3	2	1	1
<i>Salix babylonica</i>	Tree	Salicaceae	2	2	1	1

cultivated species), *Guilleminea densa* and *Schkuhria pin-nata* (naturalized species), *Cynodon dactylon* and *Eragrostis lehmanniana* (indigenous species), and *Dodonaea viscosa* and *Vigna unguiculata* (indigenous cultivated species). Wet-lands and fallow fields were found to have the least number of indigenous species, however wetlands had more natural-ized species than natural areas and fallow fields (fig. 4).

DISCUSSION

Dominant taxa

This study indicated that four of the ten most dominant fami-lies in South Africa were also dominant in Tlhakgameng. The frequent occurrence of species from these families (Asteraceae, Fabaceae, Mesembryanthemaceae and Poaceae)

can be attributed to their extensive cultivation in gardens as part of the ornamental flora and food plants (Pienaar 2000), as well as their natural richness in the Tlhakgameng envi-rons (Molebatsi 2010). The micro-climate in urban environ-ments favour many taxa from these large, diverse and adapt-able South African families (Ellis et al. 2006). Inherently the habitat template determines climate and the creation of ecologically novel habitat types predict the species composi-tion (Dos Reis et al. 2006, Lundholm & Marlin 2006), and, hence, dominant families within the settlement.

Genera of alien plant families are cultivated mostly for their high ornamental value (e.g. *Canna* and *Rosa*) and nutri-tional value (e.g. *Amaranthus* and *Prunus*). The majority of the genera recorded from Tlhakgameng are well-represented in the South African natural flora (77% of the cases), how-ever the genera of 104 recorded species are not found natu-

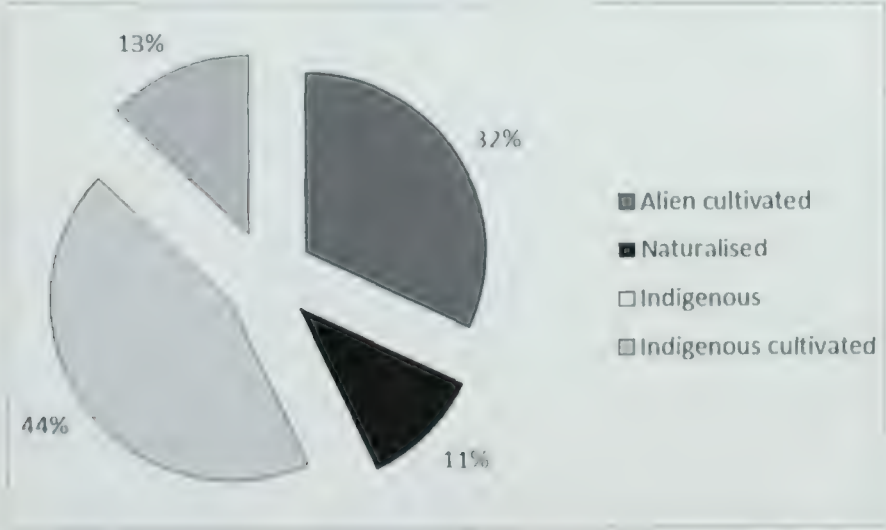


Figure 3 – The total species richness of 460 species divided up as alien cultivated, indigenous, indigenous cultivated and naturalized.

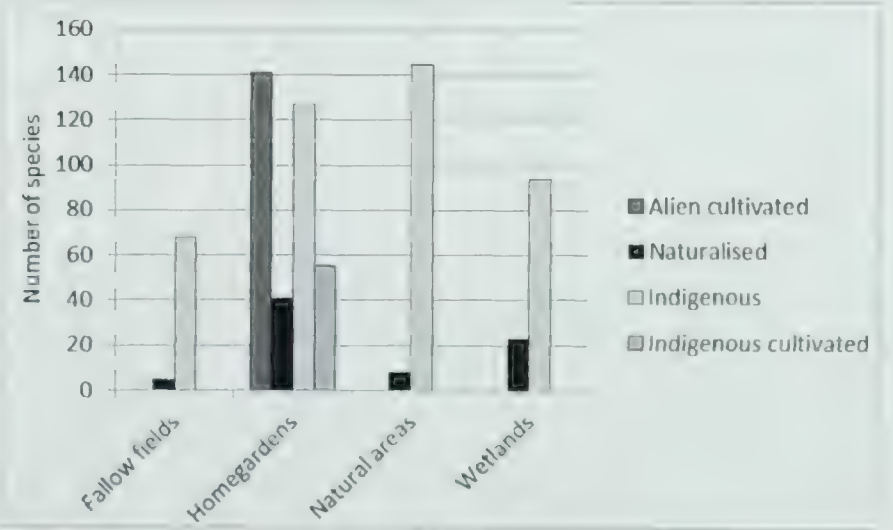


Figure 4 – Comparison of the composition of the total species richness of four different land-use types in Tlhakgameng.

rally in South Africa, e.g. *Aeonium* and *Callistemon* (Glen 2002). From the dominant genera, many species of *Solanum* and *Acacia* are popular ornamental subjects and some are declared weeds, which explain to a certain extent the frequent occurrence of these genera in gardens. In total, 43% of the species from these genera are alien to South Africa (Germishuizen et al. 2006). In the top 20 most frequently recorded species, the alien species in the list were naturalised weeds. These naturalized species may originally have been horticultural subjects that escaped from gardens into the natural surroundings (Hodkinson & Thompson 1997) and are no longer cultivated. The most frequently recorded species, the indigenous grass *Cynodon dactylon* is, however, not cultivated but regarded as an invasive species in urban wetlands (Cilliers et al. 1998) and along road verges in urban areas (Cilliers & Bredenkamp 2000) in South Africa.

Endemic and endangered species

Several rare and endangered species are often preserved in homegardens (Kabir & Webb 2008). Endemic and endangered species represent only a small portion of the garden flora, but its collective effort across entire urban ecosystems, and also globally, holds tremendous potential (Savard et al. 2000, Gaston et al. 2005). However, the cultivation of these species takes place because of its use value and not necessarily with conservation in mind (Das & Das 2005). As perceptions of what is considered useful changes over time, these plant species of conservation concern may be replaced with something new. According to Cilliers et al. (2004) urban nature conservation is not really regarded as important in South Africa, and new approaches are needed to sensitise urban residents, planners and policy makers about its importance. The presence of the rare and endangered species in homegardens corroborates the role that such land-use types can fulfill in the conservation of indigenous biodiversity, but its contribution is of temporary nature. Through interaction of gardens with other types of green space in close vicinity within the urban environment, better support of biodiversity is possible – a concept described by Colding (2007) as ‘ecological land-use complementation’. This means that more indigenous species can be supported in terms of nutrition, space and water resources by the combined patches of the entire urban green infrastructure, which stresses the importance of proper planning of urban development. Furthermore, such conservation resources that already exist can be utilised better in protecting not only endangered, but also abundant indigenous species (Hamilton 1999).

Useful plants

South Africans cultivate plants as part of their cultural heritage and because of its value e.g. food, natural healing remedies, construction material and other uses (Van Wyk et al. 1997, Van Wyk & Gericke 2000). Food plants made the largest contribution to the total flora (27%). Similarly in Ganyesa, a small rural village in the North-West Province situated 30 km away, 28% of plant species were classified as food plants (Cilliers 2010). The crop combinations found in homegardens of a region are strongly influenced by the specific needs and preferences of the household (Christanty et al.

1986) and the diversity of food plants is an indication of the dependence of poorer communities in rural settlements on nutritional complementarities with other major food sources.

Gardening in Tlhakgameng was also seen to be strongly influenced by the European culture of growing ornamentals, thus resulting in the high degree of ornamental plant species (57%) for the study area. The introduction of these species to the garden may be based on hearsay (Kumar & Nair 2004), often due to exposure as farm workers on white-owned farms. Like Tlhakgameng, inhabitants of Ganyesa also use many ornamental species for cultivation, which further corroborates that even poorer, more traditional communities regard aesthetics as important in urban greening (Cilliers 2010).

It is also important to remember that rural inhabitants make substantial use of wild resources from communal areas around their settlement (High & Shackleton 2000), as well as from arable and residential plots inside (Molebatsi et al. 2010). It has been shown that the number of medicinal plants utilized by people is higher when there are wild, uncultivated resources within the settlement (Nemudzudzanyi et al. 2010).

Origin of garden flora

Species with a widespread, natural distribution in South Africa were most common in homegardens including tree species such as *Acacia karroo*, and grass species such as *Eragrostis lehmanniana* (Germishuizen et al. 2006). Few species were contributed by the dry regions of South Africa, despite these species probably being the best adapted to the climate of the study area and would be much more water-wise (Pienaar 2000). The fact that indigenous species are present as part of cultivation practices, is ascribed to the prevailing indigenous knowledge systems of the South African indigenous people regarding important cultural plants (Molebatsi et al. 2010). In many cases, however, gardeners rather purchase the greater variety of colourful or hardy alien horticultural species available at nurseries, which are mostly alien and even invasive (Wilcove et al. 1998, Miller 2005, McKinney 2006, Marco et al. 2008).

Plant species from similar climates are adapted to specific environmental conditions such as temperature ranges, frost resistance and it would thus be able to survive such conditions elsewhere (Wezel & Bender 2003). Commonalities between the climate of the region of origin of cultivated alien species and the South African climate could be the reason why alien plants are available for cultivation in Tlhakgameng. These species are often hardier, but also lack natural enemies which makes them healthier plants. The Americas and Asia were the biggest contributors to the alien horticultural flora of Tlhakgameng homegardens, indicating that plant species from these regions are best-suited for the local climatic conditions, even hardier than most indigenous cultivated species (Henderson 2006). Apart from hardiness and suitability to grow under cultivation, these cultivated alien species also possess another important, mutual characteristic – ornamental value – that makes it popular for cultivation.

Invasive species

Apart from substantial biodiversity utilisation, maintenance and conservation taking place in gardens, there are some negative aspects, such as the occurrence of invasive alien species (Henderson 2001, Dehnen-Schmutz et al. 2007, Cilliers et al. 2008), which is further exacerbated by homegarden management practices (Richardson et al. 2000, Siebert et al. 2010). According to Richardson et al. (2005), South Africa is regarded as a country threatened by invasive alien plants. Many of these alien species have the potential to escape from cultivation to form self-sustaining natural populations (becoming naturalized) (Sullivan et al. 2005). This may have disadvantageous effects on the survival and existence of indigenous vegetation and biodiversity (Pimentel et al. 2000, Richardson & Van Wilgen 2004). The number of alien invasive species found in all land-use types of Tlhakgameng (19 species) confirmed that this is a problem of human-created ecosystems where sources of alien invasives are maintained. Most of the invasive species found in homegardens either were cultivated extensively in the past (not commercially available anymore, e.g. *Ligustrum lucidum*) or is still cultivated today (*Canna × generalis*, *Celtis sinensis* and *Pennisetum clandestinum*). The fact that many prohibited species are still cultivated unchecked in this rural settlement suggests that these species will remain problematic in the future. However, the low occurrences of most of the cultivated invasive species in gardens present limited opportunity for these species to spread outside of cultivation.

Species diversity

The higher total number of species (gamma diversity) of homegardens when compared to other land-use types is further proof of the contribution made by horticulture to the plant diversity of urban areas. Plant diversity is generally viewed as an indication and determinant of overall biodiversity, influencing all related biota (Matson et al. 1997) and the green space in urban areas are thus of critical importance for all living in these environments. According to Tilman (2000), greater plant diversity leads to greater productivity in plant communities, nutrient retention in ecosystems and ecosystem stability. However, lower plant diversity leads to greater loss of soil nutrients through leaching which ultimately decrease soil fertility and further lowering plant productivity (Tilman 2000).

The reason for more alien than indigenous cultivated species in homegardens is that cultivation practices promote the planting of hardy and aesthetic alien species and the diverse species pool that gardeners can choose from for cultivation purposes (Thompson et al. 2003, Hope et al. 2003, Kühn et al. 2004), simultaneously contributing to high species diversity. Gardens are furthermore continually supplied with nutrients and water, thus removing the constraints of survival associated with natural areas and therefore increasing the number of species that could exist in a limited environment (Niinemets & Peñuelas 2008, Hope et al. 2003). Species that would not survive the conditions of natural habitats are thus enabled to survive.

CONCLUSIONS

This study confirms that rural settlements, like urban environments, are floristically diverse (Thompson et al. 2003). The results of this study revealed that homegardens have the highest species richness as compared to other types of land-use in a rural settlement. Natural areas were found to have the second highest species richness, but they are more homogeneous than homegardens in terms of species diversity. The majority of the species found in homegardens were cultivated horticultural floras, and indigenous and alien weeds, which furthermore confirm that homegardens contain a complex plant diversity. The cultivation of alien species in homegardens further decreases the natural biodiversity of rural areas.

However, homegardens of settlements also provide a refuge for endemic or threatened species as was shown by Das & Das (2005). The majority of such species found in Tlhakgameng were cultivated in homegardens. As a result, the conservation of these species is in turn greatly dependant on the home owners, whose cultivation decisions are in turn adversely affected by modern life style and their socio-economic status. However, homegardens are floristically diverse and dynamic systems that can serve as *in situ* conservation sites. As a result, homegardens should be taken into consideration for future conservation or biodiversity management projects. According to Goddard et al. (2009) biodiversity information should be upscaled from gardens to larger landscapes because the individual gardens cover a much smaller area than that needed to be managed to ensure that viable populations are retained.

Like in other developing parts of the world (Pandey et al. 2007), homegardens sustain the growth of a rich and diverse mixture of multipurpose species, which satisfy the various needs of households in Tlhakgameng. As a result, homegardens play a significant role in subsistence for the inhabitants in Tlhakgameng. Urban agriculture should therefore not be disregarded as an opportunity to utilize the rich plant diversity of rural settlements to improve the livelihoods of the inhabitants. The multiple benefits of urban agricultural practices as part of a model of a healthy community are discussed by Cilliers (2010). The importance of gardens in terms of social-ecological interactions providing several social and ecosystem services (Goddard et al. 2009, Barthel et al. 2010, Marco et al. 2010) is often ignored. These services need to be quantified in future homegarden research and studying South African cities, which are characterized by “steep” socio-economic gradients according to Lubbe et al. (2010) will enhance our understanding of “how natural and social factors will contribute to urban biodiversity patterns” (Marco et al. 2010).

SUPPLEMENTARY DATA

Supplementary material is available in pdf at the Supplementary Data Site of publications from the National Botanic Garden of Belgium (<http://www.nbgpublisher.be> > SBB50 - folder 571) and consists of the following: (1) twenty most dominant species recorded for all land-use types in Tlhakgameng based on frequency of occurrence; (2) South African

endemic species recorded from all land-use types in Tlhakgameng based on frequency of occurrence; (3) species recorded from Tlhakgameng that are listed as threatened in the current South African Plant Red Data List; (4) origins of the alien cultivated and naturalized species in Tlhakgameng; (5) total number of species per growth form for each of the four land-use types in Tlhakgameng.

ACKNOWLEDGEMENTS

We are indebted to the National Research Foundation and African Unit for Transdisciplinary Health Research (AUTHR), North-West University, for financial support. Marie du Toit kindly prepared the locality map.

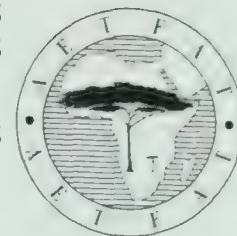
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Manuscript received 29 Oct. 2010; accepted in revised version 10 Jan. 2011.

Communicating Editor: Rainer Bussmann.



New records for the flora of Cameroon, including a new species of *Psychotria* (Rubiaceae) and range extensions for some rare species

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Background – The inventory of Cameroon's flora is far from complete and additional work is needed to document the country's extremely rich flora, and thus enhance its conservation. In this framework, botanical exploration was conducted between 2007 and 2011 in various regions of Cameroon and resulted in the discovery of several new national records and new species.

Methods – Normal practices of herbarium taxonomy have been applied. For the endemic or subendemic species, a preliminary IUCN conservation has been proposed using the IUCN criteria.

Results – A total of twelve taxa are recorded as new for the flora of Cameroon. Significant range extensions are reported for eight restricted-range species. A new species, *Psychotria yaoundensis* O.Lachenaud, endemic to Cameroon and only known from two rocky hills in the surroundings of Yaoundé, is described and illustrated. Additions to the flora of Equatorial Guinea (five species), Nigeria, Ivory Coast and the Democratic Republic of Congo (one species each) are also reported. *Psychotria moliwensis* and *Vangueriopsis gossweileri* are synonymised under *P. fernandopoensis* and *V. rubiginosa*, respectively.

Conclusion – Many areas within Cameroon remain botanically poorly explored. Our exploration highlights the importance of the Rumpi Hills, Tchabal Mbabo, and the rocky hills around Yaoundé for plant conservation. Our data will help conservationists in determining areas highly valuable for conservation.

Key words – Cameroon, Central Africa, flora, IUCN, Orchidaceae, *Psychotria*, Rubiaceae, Rumpi Hills, Tchabal Mbabo, Yaoundé.

INTRODUCTION

The Republic of Cameroon, situated on the Atlantic Coast in the Gulf of Guinea, covers 475440 km² and has such a great diversity of habitats that it is often compared to "a small Africa". The main vegetation zones, studied in detail by Letouzey (1968, 1985), are:

- an arid savanna plain situated in the extreme north, around lake Chad;
- the Adamaoua plateau, a region of hilly savannas interspersed with gallery forests, extending between c. 5°30' and 8°30'N;

- the Guineo-Congolian rainforest zone, covering the south of the country, where several forest types have been distinguished by Letouzey (op. cit.). Although mostly constituted of lowland forest, this area includes some hills up to near 1300 m with small areas of submontane forest;

- the Western Cameroon highlands, a succession of mountains stretching from Mt Cameroon, the country's highest peak (4097 m) near the coast, to the Bamenda highlands and Tchabal Mbabo in the northwest; the natural vegetation (now highly degraded in some areas) consists of submontane and montane forest up to c. 2500 m,

and montane grassland higher up; it is an important area of endemism for both plants and animals.

Although Cameroon has been better explored by botanists than most other Central African countries, its flora remains incompletely known, and several new species are described every year (e.g. Cheek et al. 2008, Sonké et al. 2008, Cheek 2009, Droissart et al. 2009a, 2009b, Sonké et al. 2009, Lachenaud & Harris 2010, Lachenaud & Séné 2010, 2012). Even among large trees, new species are regularly discovered (e.g. van der Burgt & Newbery 2006, Mackinder et al. 2010). This is partly due to the high botanical diversity of the country which includes many endemics. In addition, botanical efforts have tended to focus on some specific sites (e.g. Mt Cameroon, Mt Kupe), leaving other areas almost unexplored, especially in the north and southeast. The *Flore du Cameroun* series, started in 1960 by the Muséum National d'Histoire Naturelle in Paris, and continued by the National Herbarium of Cameroon in Yaoundé, covers only about half of the families and its publication has markedly slowed down in recent years. More recently, a national checklist, numbering 7500 indigenous or naturalized species, has been published by Onana (2011).

As a result of collaboration between the University of Yaoundé I, the National Botanic Garden of Belgium, the Université Libre de Bruxelles and the Institut de Recherche pour le Développement, we conducted fieldwork in various areas of Cameroon between 2007 and 2011. Since we were primarily interested in Orchidaceae and Rubiaceae, we focused on wet forest areas, where these two groups are most diverse. The present paper is mainly based on the results of our exploration. In addition to the description of a new species, *Psychotria yaoundensis* O.Lachenaud, we report here twelve new records (eleven species and one infraspecific taxon) for Cameroon, and important range extensions for eight other restricted species, most of which are Cameroon highland endemics.

MATERIAL AND METHODS

Main localities visited (fig. 1) cover a broad range of forest types (semi-deciduous, lowland evergreen, montane and sub-montane) and vary from well-prospected (e.g. Mt Kupe) to very little-known (e.g. Rumpi Hills, Tchabal Mbabo).

Identification of the collections was carried out based on comparison with reference specimens hosted at BR, BRLU, HBG, K, P, WAG and YA, which also provided some additional data.

We defined new records as those not appearing in the *Flore du Cameroun* or in Onana (2011).

To estimate the conservation status of the species, geo-referenced specimen data were imported into a GIS using ArcView™ software to generate the distribution map and to calculate area of occupancy (AOO) and extent of occurrence (EOO) using Cats 1.2 (Moat 2007). The cell area was set to the largest permissible value (cell width = 3.16 km). The AOO and EOO figures were used in conjunction with our field experience, Google Earth observations and literature data to assess the conservation status based on the IUCN Red List Categories criteria (IUCN 2001).

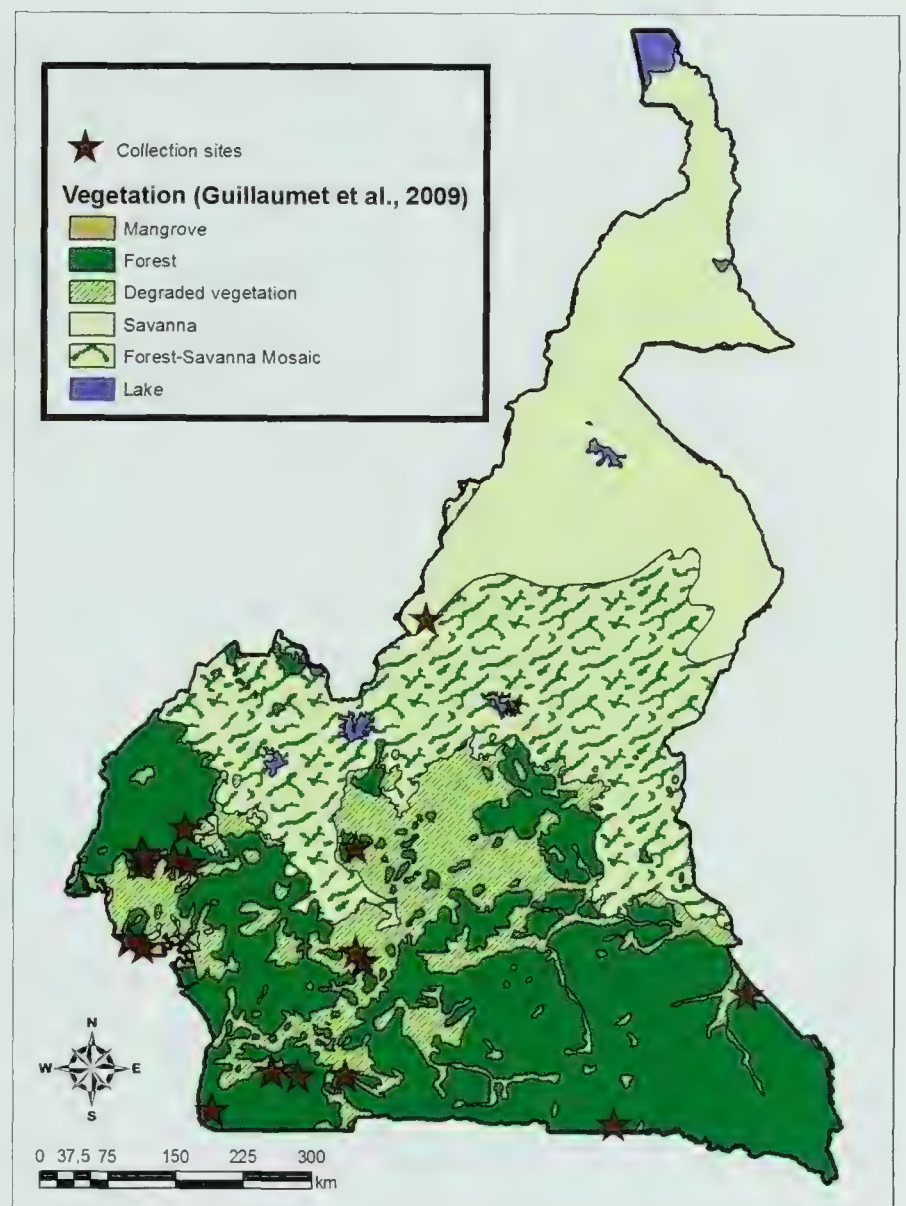


Figure 1 – Map of Cameroon indicating areas prospected by the authors between 2007 and 2011.

RESULTS

The species are arranged by alphabetical order of families, genera and species. Taxa new to Cameroon are marked with an asterisk. For each species, specimens are cited by alphabetical order of provinces. Collections from outside Cameroon are also cited if they are of particular interest. For example, new country records are reported for Nigeria (*Mussaenda epiphytica*), the Democratic Republic of Congo (*Vangueriopsis rubiginosa*), Ivory Coast (*Psychotria recurva*) and Equatorial Guinea (Bioko: *Chassalia laikomensis*, *Gaertnera letouzeyi*; Rio Muni: *Bulbophyllum calyptratum* var. *lucifugum*, *Chazaliella longistylis*, *Rutidea ferruginea*).

APOCYNACEAE (incl. Asclepiadaceae)

**Secamone erythradenia* K.Schum.

Distribution – Cameroon, Gabon, D.R.Congo, Angola, Zambia.

Ecology – A small twining liana found mainly in Zambezian savannas; in the forest zone restricted to fringing forest on inselbergs.

Notes – The only Cameroonian specimen known is sterile, but the leaves are unmistakable and identical to Gabonese material. This population, from the inselbergs of Cameroon and Gabon, is geographically separated from the main range



Figure 2 – Photographs illustrating a selection of species treated in the present paper: A, *Albucca abyssinica*, flowers; B, *Abroma angustum*, flowers and detail of fruits; C, *Ardisia atrobullata*, flowers and detail of leaf; D, *Eurychone galeandriae*, flowering plant; E, *Rhipidoglossum paucifolium*, flowering plant; F, *Polystachya riomuniensis*, flower; G, *Psychotria fernandopoensis*, flowers; H, *Stalzia repens* var. *cleristogama*, flower; I, *Chassalia laikomensis*, flowers; J, *Vangueriopsis rubiginosa*, flowers; K, *Mussaenda epiphytica*, flowers; L, *Psychotria vaouindensis*, flowers.

of the species (D.R.Congo, Angola, Zambia) and may be worth of infraspecific distinction on account of its corolla lobes shorter in relation to the tube; however, more flowering material is needed to check whether this difference is constant.

Specimen studied – **Cameroon. South Province:** Akoakas Rock, c. 35 km SE of Ebolowa, 6 May 2009, *Lachenaud et al.* 602 (BR, YA).

HYACINTHACEAE

**Albuca abyssinica* Jacq. (fig. 2A)

Distribution – Nigeria, Cameroon, D.R.Congo, and widespread in East Africa.

Ecology – A herb of rocky savanna on inselbergs.

Notes – Gledhill & Oyewole (1972) report this species from Cameroon but no specimens are cited and we have found no other mentions in literature. *A. abyssinica* is common on the summit of the Mbam Minkom massif; one plant was also seen (but not collected) on the summit of the Akoandoum hill near Yaoundé.

Specimen studied – **Cameroon. Central Province:** summit of Mbam Minkom, 29 May 2009, *Lachenaud & Taedoung* 924 (BR, YA).

MALVACEAE

**Abroma augustum* (L.) L.f. (fig. 2B)

Distribution – In Africa: Cameroon, D.R. Congo (Germain 1963).

Ecology – A ruderal shrub.

Notes – Native to south-east Asia, the species has been cultivated in many tropical countries for fiber production and became locally naturalised. Although there are apparently no published records from Cameroon, it has been present in the country since 1983 at least. So far it is known only from Lake Barombi Mbo, where it is completely naturalised. The species is potentially invasive, and Cameroonian botanists should pay attention to its possible spread. The plant is easily recognized by its leaves (which are trilobed on the main branches but entire on flowering shoots), its pendulous pinkish brown flowers with curiously clawed petals, and its 5-winged capsules covered with irritating hairs.

Specimens studied – **Cameroon. Southwest Province:** Lake Barombi Mbo near Kumba, 16 Apr. 2009, *Dessein et al.* 2542 (BR, YA); Kumba vicinity, Dec. 1983, *Thomas* 2736 (BR, MO).

MYRSINACEAE

Ardisia atrobullata Taton (fig. 2C)

Distribution – Endemic to Cameroon, only found in the coastal area near Douala and Limbe (fig. 3).

Ecology – Littoral forest on volcanic soils.

Notes – A very rare species, only known from these two collections. It is easily recognized by the very prominent dark dots on the upper surface of the leaves (hence the specific name). The pale violet anthers, of the same colour as the pet-



Figure 3 – Distribution of *Gaertnera letouzeyi*, *Vangueriopsis rubiginosa* and *Ardisia atrobullata*.

als, are also exceptional in the genus (other species have yellow anthers, as far as this is recorded).

A Gabonese specimen (*N.Hallé & Villiers* 5171), cited in the protologue of *A. atrobullata* (Taton 1979), in our opinion belongs to a new taxon, together with *Lachenaud et al.* 773 from southern Cameroon (Campo region). This taxon has the leaves conspicuously dark-dotted, like *A. atrobullata*, but markedly narrower. Unfortunately its flowers are not yet known.

Conservation status – The species is assessed as Endangered (EN B2ab(iii)) based on the restricted range (AOO = 19.97 km², EOO not calculable), the small number of locations (two) and the continued decline in habitat extent and quality (it only occurs in low-altitude forests which are under strong pressure from agriculture and urban extension).

Specimens studied – **Cameroon. Littoral Province:** Douala, route Razel km 43, 7 June 1959, *Letouzey* 2124 (holo-: P; iso-: P, WAG, YA). **Southwest Province:** Bimbria-Bonadikombo Community Forest, Elephant River, 27 Apr. 2009, *Dessein et al.* 2820 (BR).

ORCHIDACEAE

**Bulbophyllum calyptratum* var. *lucifugum* (Summerh.) J.J.Verm.

Distribution – Ivory Coast, Liberia, Sierra Leone, Cameroon, Equatorial Guinea (Rio Muni) (distribution in Lower Guinea: fig. 4).

Ecology – Epiphyte in rain forest rich in Caesalpinoideae; also found in secondary forest or in old cocoa plantation; 100–600 m.

Notes – This taxon is newly recorded from Atlantic Central Africa (Cameroon and Equatorial Guinea). However, drawings given by Zapfack (1993) and Simo (2003) show clearly that they collected specimens of this taxon but misidentified them as *B. teretifolium* Schltr. The most striking difference between the two taxa is that the pseudobulbs of *B. teretifolium* are unifoliated and perfectly terete while those of *B. calyptratum* var. *lucifugum* are bifoliated and semi-terete. Most



Figure 4 – Distribution of *Bulbophyllum calyptratum* var. *lucifugum* and *Eurychone galeandrae* in Lower Guinea.

specimens cited below are sterile, but can be identified without any doubt.

Specimens studied – Cameroon. South Province: Bidjouka (Massif de Ngovayang), 14 Jun. 2006, *Droissart* 147 (BRLU, YA); Bindem, 15 Aug. 2006, *Droissart & Simo M.* 264 (BRLU, YA); *ibid.*, 11 May 2007, *Droissart* 536 (BRLU, YA); *ibid.*, 7 Jul. 2007, *Droissart & Simo M.* 604 (BRLU, YA); *ibid.*, 22 Jul. 2008, *Simo M. & Sonké* 83 (BRLU, YA); *ibid.*, 22 Jul. 2008, *Simo M. & Sonké* 84 (BRLU, YA); Nkolembonda, 15 Mar. 2008, *Simo M. & Sonké* 16 (BRLU, YA). **Southwest Province:** Sanctuaire de Banyang Mbo, village de Nguti, 15 Mar. 2004, *Stévant et al.* 2152 (BRLU, YA); *ibid.*, 17 Mar. 2004, *Stévant et al.* 2175 (BRLU, YA); *ibid.*, village de Bejange, 1 Feb. 2008, *Droissart* 643 (BRLU, YA).

Equatorial Guinea. Rio Muni: inselberg de Bicurga, 31 May 2002, *Stévant* 1598 (BRLU).

**Eurychone galeandrae* (Rchb.f.) Schltr. (fig. 2D)

Distribution – Ivory Coast, Cameroon, Central African Republic, Gabon, Republic of Congo, D.R. Congo, Angola (distribution in Lower Guinea: fig. 4).

Ecology – Epiphyte in semi-deciduous forest rich in Sterculiaceae and Ulmaceae. In Cameroon, only one individual was found growing on a branch with a diameter of 15 cm, partially covered with moss.

Specimen studied – Cameroon. East Province: Bitonga, 25 km à l'E de Yokadouma, 4 Oct. 2009, *Droissart* 652 (BRLU, YA).

**Polystachya riomuniensis* Stévant & Nguema (fig. 2F)

Distribution – Cameroon, Equatorial Guinea (Rio Muni) (fig. 5).

Ecology – Epiphyte in lowland and submontane moist forest, 500–1200 m. In Rio Muni, specimens were collected in the forest fringe and saxicolous forest of an inselberg (Stévant & Nguema 2004).

Specimens studied – Cameroon. South Province: Sud du village d'Akom II, 21 May 2008, *Simo M. et al.* 44 (BRLU, YA); *ibid.*, 20 Sept. 2008, *Simo M. et al.* (Ombrière de Yaoundé) 1336 (BRLU, YA); *ibid.*, 24 Sept. 2008, *Simo M. et al.* (Ombrière de Yaoundé)

1348 (BRLU, YA); *ibid.*, 9 Feb. 2009, *Simo M. et al.* (Ombrière de Yaoundé) 1466 (BRLU, YA).

**Rhipidoglossum paucifolium* D.Johanss. (fig. 2E)

Distribution – Liberia, Cameroon (distribution in Cameroon: fig. 5).

Ecology – Epiphyte collected along riverside forest.

Notes – Previously known only from the type specimen collected on Mount Nimba, Liberia. The species' discovery in Cameroon considerably extends its range. The species is now considered as an Upper Guinea-Lower Guinea linking species.

Specimens studied – Cameroon. Southwest Province: Sanctuaire de Banyang Mbo, à environ 500 m du village Babubok, 4 Jun. 2008, *Simo M. et al.* (Ombrière de Yaoundé) 1090 (BRLU, YA).

Stolzia repens (Rolfe) Summerh. var. *cleistogama* Stévant, Droissart & Simo (fig. 2H)

Distribution – Cameroon (fig. 5).

Ecology – Epiphyte in moist submontane forest.

Notes – This recently described taxon (Droissart et al. 2009a) was only known from three localities in the South and Central provinces. Its discovery in the Southwest province is therefore a significant range extension. It is a tiny epiphytic plant, and therefore easily overlooked.

Conservation status – A preliminary assessment as Endangered was provided by Droissart et al. (2009a), but the important range extension reported here call for a re-examination of this status. It is now known from five locations, all situated outside protected areas. The species has an EOO of 34928.24 km² and an AOO of 49.93 km². However, its habitat is extremely fragmented (submontane forest) and the area of this vegetation is continually decreasing. We therefore propose to keep the species as Endangered (EN) under B2ab(iii) criteria.



Figure 5 – Distribution of *Polystachya riomuniensis*, *Rhipidoglossum paucifolium* and *Stolzia repens* var. *cleistogama* in Lower Guinea.

Specimens studied – Cameroon. Southwest Province: Rumpi Hills near Dikome Balue, 19 Apr. 2009, *Dessein et al.* 2595 (YA); Mt Etinde above Etome, 28 Apr. 2009, *Dessein et al.* 2850 (YA). **Central Province:** Mbam-Minkom (région au NO de Yaoundé), village de Nyemeyong, sommet d'une colline à l'O du village, alt. 1115 m, 13 May 2006, *Droissart* 68 (BRLU, MO, YA); *ibid.*, 14 Apr. 2008, *Simo M. et al.* (*Ombrière de Yaoundé*) 1002 (BRLU); Mefou, 22 miles Yaoundé on Akonolinga road, 19 Oct. 1968, *Sanford* 5204 (YA). **South Province:** Akom II (route Kribi-Ebolowa), sommet de la colline située à 8km au S du village, alt. 1065 m, 24 Apr. 2007, *Droissart & Simo M.* 427 (BRLU); *ibid.*, 24 May 2008, *Simo M. et al.* 51 (BRLU).

RUBIACEAE

Chassalia laikomensis Cheek (fig. 2I)

Distribution – Nigeria, Cameroon, Equatorial Guinea (Bioko) (fig. 6).

Ecology – A shrub in submontane and montane forests, (1100–)1300–2400 m, where it is often the dominant species.

Notes – This recently described species was known only from the Bamenda highlands (Cameroon) and Chappal Hendu (Nigeria) (Cheek & Csiba 2000). It has since been found on Bioko, and in most submontane areas of western Cameroon, including Mt Cameroon, Mt Etinde (rare), the Rumpi Hills (where particularly abundant, dominating the shrub layer in submontane forest), Mt Kupe (abundant), the Mbam massif and Tchabal Mbabo. An isolated population occurs on the summit of the Mbam Minkom massif, near Yaoundé. The species is quite variable, evidently in relation with altitude; plants from Mt Cameroon, initially thought to be a different taxon (Cheek & Csiba 2000), are here considered conspecific. The Bioko specimens have been misidentified as *C. cristata* (Hiern) Bremek. or *C. pteropetala* (K.Schum.) Cheek; all collections cited under these names by Davis & Figueiredo (2007) belong to *C. laikomensis*.

Conservation status – Hitherto regarded as Critically Endangered A2c (IUCN 2011) but the discovery of new and important populations, call for a revision of its conservation status. The species qualifies for EN under the AOO criterion (AOO = 229.67 km²) and LC under the EOO criterion (EOO = 266918.19 km²). It is known from more than ten locations and is abundant in some of them. Some of the locations are severely degraded, but others are still intact and protected at different degrees. Since some of the subpopulations may disappear due to deforestation in the near future, we propose to classify the species as near threatened (NT).

Specimens studied – Cameroon. Central Province: Sommet du Mbam Minkom, alt. 1243 m, 29 May 2009, *Lachenaud & Taedoung* 929 (BR, YA). **Northwest Province:** Tchabal Mbabo, alt. 2063 m, 9 May 2009, *Dessein & Taedoung* 2966 (BR, YA). **Southwest Province:** Mt Cameroon, 7 Feb. 1969, *Breteler et al.* MC 291 (WAG, YA); Rumpi Hills near Dikome Balue, alt. 1408 m, 18 Apr. 2009, *Dessein et al.* 2559 and 2562 (BR, YA); *ibid.*, alt. c. 1400 m, 19 Apr. 2009, *Dessein et al.* 2588 (BR, YA); Mt Kupe above Nyassosso, alt. 1360 m, 24 Apr. 2009, *Dessein et al.* 2727 (BR, YA); Mt Etinde, above Etome, alt. 1601 m, 28 Apr. 2009, *Dessein et al.* 2842 (BR, YA); Mt Cameroon, 18 Mar. 1969, *Ekeme* 14 (YA); Mounts Rumpi - Rata Mt, 2 km SW Dikome Balue, 24 Mar. 1976, *Letouzey* 14573 (BR, K, P, YA); versant NW du Mont Kupe, 25 Apr. 1976, *Letouzey* 14691 (BR, P, YA); summit of Mt Kupe, 30 Nov. 1985, *Thomas & MacLeod* 5078 (YA); above Mbilishe, 7 May 1987,



Figure 6 – Distribution of *Chassalia laikomensis*.

Thomas et al. 7439 (K, WAG). **West Province:** Nkoutoupi, Mbam massif, 1 Apr. 1983, *Goetghebeur* 4973 (YA).

Equatorial Guinea. Bioko: Malabo - Pico Basilé, road km 14–15, 5 May 1987, *Carvalho* 2893 (K); Malabo - Pico Basilé, Pico road km 11–12, 8 Aug. 1988, *Carvalho* 3559 (K); s.l., s.d., *Fernandez Casas* 10211 (K) & 11926 (K); entre Moca y el lago Biao, 15 July 1986, *Fernandez Casas* 10389 (BR, K, S, WAG); s.l., s.d., *Mann* 310A (K); above Moka, 8 Sep. 1959, *Wrigley & Melville* 578 (BM, K, P).

**Chazaliella longistylis* (Hiern) E.M.A. Petit & Verdc.

Distribution – Cameroon, Equatorial Guinea (Rio Muni), Gabon.

Ecology – A shrub, restricted to littoral forests on sandy soils.

Notes – Previously known only from two collections in Gabon (Verdcourt 1977), the species is in fact locally common in this country. It is newly recorded from Cameroon (where apparently uncommon) and Equatorial Guinea.

Specimens studied – Cameroon. South Province: km 27 Kribi – Ebolowa, 27 Jan. 1970, *Bos* 6177 (BR, P, WAG, YA); 20 km S Kribi, 7 Feb. 1983, *De Namur* 2150 (YA); km 28 Kribi – Campo, 1 Dec. 1998, *J.J. de Wilde et al.* 12055 (WAG); Likodo river, Ebodje, 8 Mar. 2001, *van Andel et al.* 3231 (WAG).

Equatorial Guinea. Rio Muni: Bata - Pembe: Estrada kms 22–23, 15 Feb. 1993, *Carvalho* 5251 (WAG); Etembue (Réserve de Ndote), 18 Aug. 1997, *Eneme & Lejoly* 44 (BRLU); Ndote, 6 Jun. 1999, *Eneme* 282 (BRLU); Jandje, 29 Jul. 1999 *Eneme* 465 (BRLU); Estuaire du Rio Muni, village Mayang, 14 Sep. 1997, *Lisowski* M-790 (BRLU)

Gaertnera letouzeyi Malcomber

Distribution – Cameroon (Southwest Province) (fig. 3).

Ecology – A shrub of primary forest undergrowth, up to 1100 m in altitude.

Notes – A recently described species (Malcomber & Taylor 2009), hitherto only known from two collections around Mamfe and one in Korup N.P. It is here newly recorded from Bioko island, Mokoko F.R. and the Rumpi Hills. In the latter

locality it was not rare around 1100 m but apparently absent from submontane forest higher up.

Conservation status – The species qualifies for Vulnerable under criterion EOO (8529.77 km²) and Endangered under AOO (69.8992 km²). It is known from six locations, most of which are unprotected (only one is in a national park) and occurs at the lower altitudes where the forest is most threatened by deforestation. It is therefore considered as Endangered EN B2ab(iii).

Specimens studied – **Cameroon. Southwest Province:** Rumpi Hills near Dikome Balue, alt. 1107 m, 21 Apr. 2009, *Dessein et al.* 2676 (BR, YA); Mokoko F.R., 2 May 1994, *Sonké* 1133 (BR).

Equatorial Guinea. Bioko. C. UPM/C. Hormiga, 18 Mar. 2007, *Galán & Barberá* 4760 (BR); C. Hormiga/C. Peter, 19 Mar. 2007, *Galán & Barberá* 4773 (BR).

Mussaenda epiphytica Cheek (fig. 2K)

Distribution – Nigeria, Cameroon (fig. 7).

Ecology – An epiphytic shrub (sometimes becoming ± lianescent) growing in the canopy of submontane and montane forests, 530–1650 m in altitude.

Notes – A recently described species, hitherto only known from Mt Kupe and nearby Bakossi Mts (Cheek 2009). It is here recorded from the Rumpi Hills, Mt Etinde, and the Mbam-Minkom massif near Yaoundé. A collection from Nigeria (unfortunately without locality) is also a new record for that country. The flowers, described by Cheek (2009) as “orange-white”, are, in our experience, always pale sulphur yellow. A white enlarged calyx-lobe is usually present, but our two collections from Mt Etinde lack it; since they are otherwise identical, we regard this as individual variation.

Conservation status – The species was treated as Vulnerable by Cheek (2009). The EOO (15601.7 km²) indeed suggests a Vulnerable status, but is not a very relevant criterion for a montane species with highly fragmented range, and under AOO (69.8992 km²) the species qualifies for Endangered (these evaluations are based on Cameroon localities only, since the exact locality in Nigeria is unknown). It is known

from six locations, and a decline in habitat extent and quality is occurring at the lower limit of its altitudinal range. We therefore propose to treat the species as Endangered under criteria B2ab(iii).

Specimens studied – **Cameroon. Central Province:** Mbam-Minkom, village de Nye-Meyong, sommet de la colline située au N-NE du village, alt. 1165 m, 27 Jul. 2006, *Droissart & Simo M.* 234 (BRLU). **Southwest Province:** Rumpi Hills near Dikome Balue, alt. c. 1400 m, 19 Apr. 2009, *Dessein et al.* 2589 (BR, K, MO, P, WAG, YA); Mt Kupe above Nyassosso, alt. 1658 m, 24 Apr. 2009, *Dessein et al.* 2742 (BR, YA); Mt Etinde above Etome, alt. 1601 m, 28 Apr. 2009, *Dessein et al.* 2841 (BR, YA); *ibid.*, alt. 531 m, 29 Apr. 2009, *Dessein et al.* 2887 (BR).

Nigeria: s.l., s.d., *van Meer* 1840 (WAG).

Oxyanthus okuensis Cheek & Sonké

Distribution – Cameroon (fig. 7).

Ecology – A shrub or small tree of montane forest, 1825–2200 m.

Notes – A Cameroon highland endemic, so far only known from Lake Oku and nearby Ajung forest (Cheek & Sonké 2000). Its discovery in Tchabal Mbabo is of importance, since, in contrast with the severely degraded Oku region, the forests of Tchabal Mbabo are largely intact.

Two collections from the Rumpi Hills, *Dessein et al.* 2631 (BR, MO, YA) and 2638 (BR, MO, YA) also probably belong to *O. okuensis*. Fruits of the latter collection, still immature, lack the typical beak of the species, but appear to be pathological: they are developing under closed flower buds, and a dissection revealed the presence of small insect larvae.

Conservation status – The species is listed as Critically Endangered A1c, B1+2b, C2a, D (Cheek & Sonké 2000, Cheek & Pollard 2000). It was known from a single, highly degraded location (Cheek & Sonké 2000). With the discovery of a second population, its status should be reevaluated as Endangered, based on criteria B1ab (iii)+2ab(iii) (EOO = 1300.14 km², AOO = 29.96 km²; number of locations = 2, decline in habitat extent and quality).

Specimen studied – **Cameroon. Northwest Province:** Tchabal Mbabo, alt. 1826 m, 10 May 2009, *Dessein & Taedoumg* 2993 (BR, MO, YA) and 2995 (BR, MO, WAG, YA).

Psychotria darwiniana Cheek

Distribution – Cameroon (Southwest Province) (fig. 8).

Ecology – A shrub of submontane forest undergrowth, (850)1000–1650 m.

Notes – A recently described species, so far only known from Mt Kupe (where it is very abundant), the Bakossi Mts, and Mt Ekomané (Cheek et al. 2008). We also found it in the Rumpi Hills, where it is rare, at least in the area visited.

Conservation status – The species was assessed as Vulnerable (VU B2ab(iii)) by Cheek et al. (2008). We suggest to consider it as Endangered (EN B1ab(iii) +2ab(iii)) based on the restricted EOO (1440.97 km²), AOO (99.86 km²), the number of locations (four), and the decline in habitat extent and quality (deforestation is ongoing in the lower part of its altitudinal range).

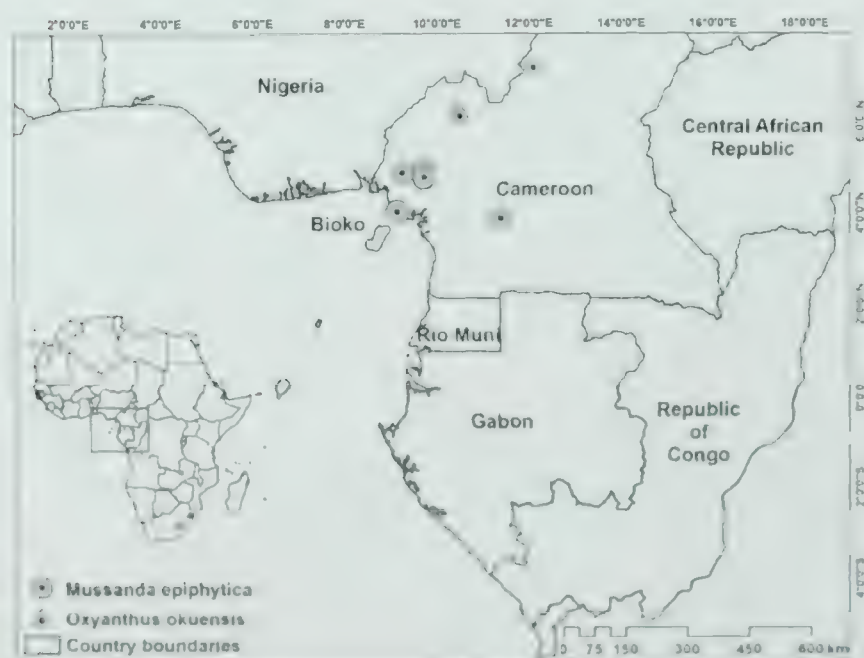


Figure 7 – Distribution of *Mussaenda epiphytica* and *Oxyanthus okuensis*

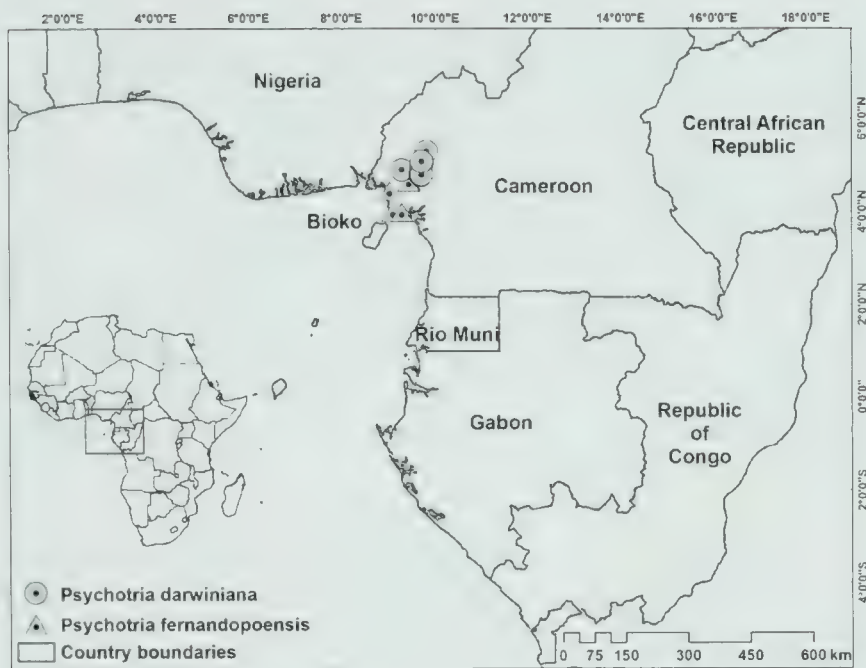


Figure 8 – Distribution of *Psychotria darwiniana* and *P. fernandopoensis*.

Specimen studied – **Cameroon. Southwest Province:** Rumpi Hills near Dikome Balue, alt. 1101 m, 21 Apr. 2009, *Dessein et al.* 2682 (BR, MO, WAG, YA).

Psychotria fernandopoensis E.M.A. Petit (fig. 2G)

Psychotria moliwensis Bridson & Cheek, **syn. nov.**

Distribution – Cameroon, Equatorial Guinea (Bioko) (fig. 8).

Ecology – A shrub of high forest undergrowth.

Notes – The type of *P. moliwensis* (*Watts* 110 from Cameroon) has large leaves and inflorescences almost completely surrounded by the stipules, while the type of *P. fernandopoensis* (*Mann* 223 from Bioko) has smaller leaves and a larger inflorescence much exceeding the stipules. At first sight these specimens look very different, but new collections showed that the inflorescence character varies within the same locality, and independently of leaf size. Therefore, we recognize only one polymorphic species.

Conservation status – *Psychotria moliwensis* is listed as Critically Endangered A2c+3c+4c (IUCN 2011). We here propose to classify *P. fernandopoensis* as Endangered (EN B1ab(iii) & B2ab(iii)) based on the restricted EOO (2221.30 km²) and AOO (79.88 km²), the small number of locations (three) and the continued decline in habitat extent and quality (it only occurs in lowland forests which are under strong pressure). It is close to classifying as Critically endangered, since two of its Cameroonian localities (Lake Barombi Mbo, Bimbia-Bonadikombo forest) have already experienced much forest clearance, while the third (Mokoko F.R.) is also threatened by logging (M.Cheek, pers. comm.). The Bioko population is possibly extinct as there have been no records for 150 years.

Specimens studied – **Cameroon. Southwest Province:** Bimbia-Bonadikombo Community Forest, Elephant River, 27 Apr. 2009, *Dessein et al.* 2822 (BR, MO, YA); S shore of Lake Barombi Mbo, 9 Nov 1986, *Manning* 766 (YA); E shore of Lake Barombi Mbo, 14 Nov. 1986, *Manning* 826, 829 & 838 (all YA); *ibid.*, 15 Nov. 1986, *Manning* 852 (YA); Victoria [=Limbe], Apr. 1899, *Schlechter* 12374 (K); Mokoko F.R., 1 May 1994, *Sonké* 1097 (K); slopes of

Barombi Mbo Crater, Kumba, Mar. 1986, *Thomas* 5703 (K, YA); E side of Barombi lake, Kumba, 26 Mar. 1986, *Thomas* 5947 (YA); Mabeta, 26 Mar. 1992, *Watts* 110 (K, holotype of *P. moliwensis*, WAG isotype).

* *Psychotria recurva* Hiern

Distribution – Ivory Coast (see below), Nigeria, Cameroon, Equatorial Guinea (Bioko) (distribution in Lower Guinea: fig. 9).

Ecology – A small shrub in lowland and submontane forest, up to c. 1400 m in altitude.

Notes – The species was only known from three collections from Bioko and Nigeria (Petit 1966), but proved to be common in the Rumpi Hills. It is obviously under-collected due to uncommon flowering. The narrow leaves with strongly undulate margin allow identification when sterile. The species is also newly recorded from Ivory Coast, which constitutes a considerable range extension westwards.

Conservation status – The species is assessed as Vulnerable (VU B2ab(ii, iii)) based on the restricted range (AOO = 69.90 km², within the limits of Endangered; EOO not relevant here since the range is disjunct), small number of localities (six) and continued decline in AOO and habitat extent and quality. It might qualify as Endangered, since the Ivory Coast population is possibly extinct now, the Haute-Dodo forest having been largely destroyed (G. Koffi pers. comm.). Of the known locations, only the Rumpi Hills (and possibly the Bioko locality) seem to be less threatened.

Specimens studied – **Cameroon. Southwest Province:** Ekombe-Mofako, Mokoko F.R., 21 Apr. 1994, *Acworth* 151 (K); Rumpi Hills near Dikome Balue, alt. 1325 m, 17 Apr. 2009, *Dessein et al.* 2550 (BR, MO, YA); *ibid.*, alt. 1417 m, 18 Apr. 2009, *Dessein et al.* 2575 (BR, YA); Mokoko F.R., Dikome, 5 May 1994, *Ekema et al.* 937 (K). **West Province:** Plaine des Mbos, 14 km S Dschang, 17 Dec. 1981, *Nkongmeneck* 196 (BR, YA).

Ivory Coast. F.C. de la Haute Dodo, 7 May 1999, *Jongkind* 4561 (WAG).



Figure 9 – Distribution of *Psychotria recurva* and *P. yaoundensis* in Lower Guinea.

**Psychotria yaoundensis* O.Lachenaud, *Pl. Ecol. Evol.* 146: 129 (2013).

Capitulis involucratis sect. *Involucratae* E.M.A.Petit & Verdc. pertinens; bracteis liberis habituque suffruticoso 15–30 cm alto *P. nodiflorae* O.Lachenaud & D.J.Harris, *P. schnellii* (Aké Assi) Verdc. et *P. mwinilungae* Verdc. valde affinis; sed a primo differt inflorescentiis terminalibus et solitaris (nec axillaribus et saepe geminatis), alabastraeque glabro et haud corniculato; a secundo et tertio bracteis angustioribus, acutis et conspicue plicatis distinguitur. Type – Cameroon, Central Province, Nkolbisson (ouest de Yaoundé), colline Akoandoum derrière l'I.R.A.D., 31 May 2009, Lachenaud 950 (holo-: BR; iso-: WAG, YA).

Undershrub, creeping at base, 15–30 cm high. **Stems** slender (1–2 mm thick), densely appressed-pubescent. **Stipules** pale green to brownish green, narrowly elliptic, 4.5–10 × 1.5–5 mm, free, deeply bifid at apex with acute and narrow lobes, weakly carinate at base, densely appressed-pubescent, caducous. **Leaves** with petiole 0.3–1(–1.7) cm long, shortly appressed pubescent; lamina elliptic to slightly obovate, 7–11.5 × 2.6–6 cm, acute at base, acuminate at apex, papyraceous, puberulent on nerves beneath, otherwise glabrous, dark green above and pale green beneath, drying brownish green with underside paler; midrib flat or very weakly impressed above; lateral nerves 10–14 pairs, weakly impressed above, conspicuously arching 1–3 mm from margin; tertiary veins densely reticulate but weakly contrasting beneath; no domatia or bacterial nodules. **Inflorescences** terminal, capitate and involucre, held horizontally, 7–15 flowered; peduncle extremely short (< 0.2 cm), glabrous or pubescent towards apex, hidden by the stipules; involucre pale green, consisting of 2–4 unequal pairs of bracts, arranged star-like (when viewed from above) and long exceeding the flowers; bracts free, entire, narrowly ovate to lanceolate, acute and longitudinally plicate at apex, shortly ciliate on margins, otherwise glabrous, the outer pair (largest) 6.5–8 × 3–6 mm. **Flowers** subsessile, 5-merous (probably heterostylous but only the short-styled morph is known); calyx very short, c. 0.5 mm long, irregularly and minutely denticulate, shortly ciliate on the margin; corolla white on both side (apex of buds pale green), with narrow tube c. 6.5 × 2 mm and reflexed lobes 2.5–3 mm long, glabrous outside, hairy inside in upper third of tube just below throat; anthers pale buff, 1.5 × 0.6 mm, on slender white filaments exceeding throat by c. 1.5 mm; style white, c. 6 mm long, pubescent at apex, just reaching corolla throat. **Fruits** only known in very young stage, pale green, ellipsoid, c. 5 × 3.5 mm, smooth, shortly and very sparsely pubescent, subsessile (pedicels probably elongating later), topped with persistent calyx. Figs 2L & 10.

Distribution – Cameroon. Only known from two neighbouring hills in the outskirts of Yaounde (fig. 9). It has not been found from other sites in the vicinity, e.g. the relatively well-collected Mbam-Minkom massif.

Ecology – Undergrowth of degraded semi-deciduous rain-forest, on granitic hills with numerous rocky outcrops, c. 750–900 m in altitude.

Conservation status – The species is assessed as Critically Endangered (CR B2ab(iii)) based on its highly restricted range (AOO estimated to be <10 km²), its occurrence in only

one location, and the continuing decline in extent and quality of habitat. It is found only in the immediate vicinity of Yaoundé, and is severely threatened by agriculture and urban expansion; the forests where it occurs are already reduced to very small degraded remnants. The following recommendations are made for its conservation: (1) measures should be taken to prevent agriculture and building on steep hills slopes around Yaoundé (which, besides threatening the endemic flora, also seriously increases the risk of floods); (2) *ex situ* cultivation from cuttings should be attempted. In addition, other hills in the area should be prospected in attempt to locate new populations.

Notes – This species belongs to sect. *Involucratae* E.M.A. Petit & Verdc., which is recognized by its flowers grouped in involucre heads. Within this group it closely resembles *P. schnellii* (Aké Assi) Verdc. from West Africa, *P. mwinilungae* Verdc. from Zambia, and the recently described *P. nodiflora* O.Lachenaud & D.J.Harris from the Congo Basin. All four species share free bracts and a low rhizomatous habit. *Psychotria nodiflora* has axillary and usually paired inflorescences (a unique condition within the genus) and its flower buds are corniculate and pubescent at apex (Lachenaud & Harris 2010). In contrast, *P. yaoundensis* has terminal and solitary inflorescences, and glabrous rounded flower buds. From the two other species, *P. yaoundensis* differs in having relatively narrow, longitudinally plicate bracts that long exceed the capitulum, rather than broad bracts closely surrounding the capitulum.

It is very remarkable that *P. yaoundensis* has not been collected before, although it grows in the immediate vicinity of Yaoundé. This is probably due in part to its low habit, but it also shows that the Yaoundé area is not as well-known as previously thought (Simo et al. 2009). The rocky habitats on hill tops and upper slopes, botanically the most interesting, appear to have been somewhat neglected by previous collectors. In view of the city's growth, there is an urgent need for exploration and conservation of these habitats (see Discussion).

Other specimen studied – Cameroon. Central Province: Nkolbisson, colline Mbogdoum derrière l'Université Catholique, 3 May 2009, Lachenaud 592 (BR, YA).

**Rutidea ferruginea* Hiern

Distribution – Cameroon, Equatorial Guinea (Rio Muni), Gabon.

Ecology – The Cameroon specimen was collected on the bank of a river in lowland forest.

Notes – The species is also new to Equatorial Guinea. *Rutidea ferruginea* is closely related to the much more widespread *R. olenotricha* Hiern. The key difference lies in the bracteoles (conspicuous, linear and exceeding the calyx in *R. ferruginea*, very short in *R. olenotricha*). Another character used by Bridson (1978), the domatia, proves unreliable: several specimens of *R. ferruginea*, including ours, have domatia similar to those of *R. olenotricha*.

Specimens studied – Cameroon. South Province: SE of Nkoadjap; c. 20 km E of Campo, 15 May 2009, Lachenaud et al. 749 (BR, MO, WAG, YA).

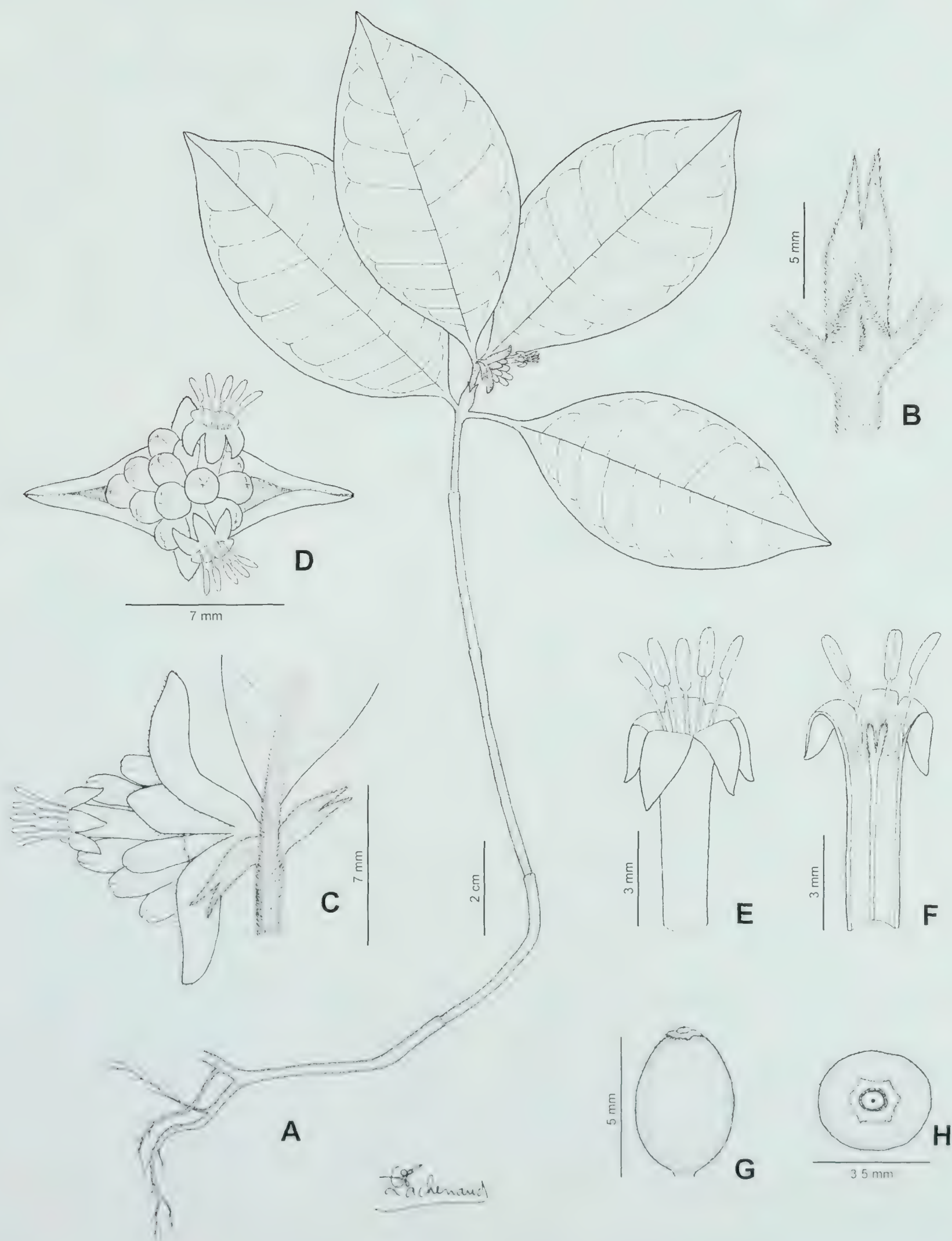


Figure 10 – *Psychotria yaoundensis*. A: habit; B: stipule; C: top of stem with inflorescence; D: inflorescence from above; E: corolla; F: longitudinal section of corolla; G: immature fruit, side view; H: immature fruit, from above. Drawing based on *Lachenaud* 950 (A–F) & *Lachenaud* 592 (G–H).

Equatorial Guinea. Rio Muni: de Sendje à Ongamnsok, 20 Feb. 2001, *Lejoly* 01/93 (BRLU); Estuaire du Río Muni, Mandjani, 8 Oct. 1997, *N. Nguema* 96 (BRLU); SO du Parc National de Monte Alén, sur la piste du rio Uolo au transect Ecofac de Mosumo, 6 Feb. 2001, *Senterre & Ngomo* 64 (BRLU).

**Vangueriopsis rubiginosa* Robyns (fig. 2J)

Vangueriopsis gossweileri Robyns, **syn. nov.**

Distribution – Cameroon, Equatorial Guinea (Rio Muni), Gabon, Republic of Congo, D.R.Congo, Angola (Cabinda) (fig. 3).

Ecology – A tree of evergreen lowland forest, 0–950 m in altitude.

Notes – We consider that *V. rubiginosa* and *V. gossweileri* are the same species, as already suspected by Verdcourt (1987). The main supposed difference between them, the number of locules in the ovary (Robyns 1931), proves to be non-existent: reexamination of the type of *V. rubiginosa* (Lecomte C56, P) shows the ovary is 5-locular, as in *V. gossweileri*, and not 2-locular as stated by Robyns (1928). Other differences cited by Robyns (1931) are minor and represent individual variation. *V. rubiginosa* is the older name.

V. rubiginosa is also newly reported from D.R.Congo, and since the species is very little-known we found it useful to give below a complete list of specimens. Despite a wide distribution, it appears to be very rare and always occurring as isolated trees (Raponda-Walker & Sillans 1961, F. Dowsett-Lemaire pers. comm., and pers. obs.). It may flower as a small tree of c. 6 m high (*Lachenaud et al.* 827) but is more commonly a medium-sized tree, 20–25 m high. The tree is very conspicuous due to its bark (very flaky, dull red-brown on young trees, becoming red and smooth on larger trees when the flakes are shed to reveal the inner layer). The regular horizontal branching and pale green drooping foliage are also unusual. The flowers are very fragrant.

Specimens studied – **Cameroon. South Province:** near Kribi, 12 Apr. 1928, *Hédin* 1699 (P); km 34 road Campo – Kribi, 17 May 2009, *Lachenaud et al.* 827 (BR, YA); Nkolebenga, colline au NW d'Ebianemeyong, 11 Apr. 1970, *Letouzey* 10363 (BR, P).

Equatorial Guinea. Rio Muni: Parc National de Monte Alén, près du village de Monte Alén, 14 Mar. 2002, *Senterre et al.* 2842 (BRLU); Nkolentangan, 11 Apr. 1908, *Tessmann* 338 (K).

Gabon: Ezanga-Offoubou, 5 Mar. 1953, *Corbet* SRF 1048 (P); Lac Ezanga, 2 Jun. 1953, *Corbet-Grandez* SRF 1069 (P); Mbel, Jan. 1968, *N. Hallé* s.n. (P); Inganga, 20 May 1914, *Le Testu* 1747 (P); Nyoŷ, 11 Apr. 1926, *Le Testu* 5913 (P); Lastoursville, 13 May 1929, *Le Testu* 7326 (P); Ebé, 21 May 1933, *Le Testu* 9152 (P).

Congo (Brazzaville): Mayombe à Goumina (Sounda), 28 Nov. 1990, *Dowsett-Lemaire* Ecol 432 (BR); Tchisseka (lac Nanga), 19 Apr. 1991, *Dowsett-Lemaire* 1582 (BR); Niounvoux, 14 Jan. 1894, *Lecomte* C 56 (P, type of *V. rubiginosa*); Bilala, 16 Apr. 1990, *Nkounkou* 96 (BR).

Angola. Cabinda: Belize, 24 Mar. 1917, *Gossweiler* 7077 (BM, type of *V. gossweileri*).

D.R.Congo: Sumbi, Feb. 1949, *Flamigni* 10116 (BR); Nsemendwa, 18 May 1957, *Jans* 1087 bis (BR); Botchumi near Nsemendwa, 1 Dec. 1958, *Jans* 1094 (BR); *ibid.*, 13 Sep. 1959, *Jans* 1094 bis (BR).

SAPOTACEAE

**Pradosia spinosa* Ewango & Breteler

Distribution – Cameroon, Gabon, Republic of Congo, D.R.Congo.

Ecology – Occurs sporadically in various types of forest, either riparian (*Sonké & Zemagho* 5561) or hilly (*Letouzey* 10862), including *Gilbertiodendron dewevrei* formations (*Letouzey* 8475).

Notes – A recently described species, easily distinguished from other African Sapotaceae by the spines on the trunk. Initially described from D.R.Congo, it has since been found in Gabon and the Republic of Congo (Gillet & Doucet 2012).

Specimens studied – **South Province:** près rivière Fom, 12 km E Kamelon (5 km SE Sangmelima), 24 Nov. 1966, *Letouzey* 8475 (YA). **Littoral Province:** NW Ndoknabao, 30 km SW Ndikinimeki, 18 Dec. 1971, *Letouzey* 10862 (YA). **Southwest Province:** Sanctuaire Mbanyang Mbo, Nguti (05°20'38.3"N 09°31'02.4"E), 5 Apr. 2011, *Sonké & Zemagho* 5561 (BR, BRLU, K, MO, P, WAG, YA).

DISCUSSION

Our results show that much remains to be known about the flora of Cameroon, and demonstrate the interest of some previously neglected localities.

The Rumpi Hills are a chain of hills (the highest of which, Mt Rata, reaches 1764 m) situated north-west of Kumba and west of the Mungo River, which separates them from the Bakossi Mts to the east. This area, little-known botanically, proved very interesting, yielding about half of our new records. Botanically the Rumpi Hills are very close to the Kupe-Bakossi region, and appear to be part of the same area of endemism. Endemic species that are shared between the Rumpi Hills and the Kupe-Bakossi region, but absent from Mt Cameroon to the south or the Bamenda highlands to the north, include *Impatiens letouzeyi* Grey-Wilson, *Justicia leucoxiphus* Vollesen, Cheek & Ghogue, *Psychotria darwiniana*, another new species of *Psychotria* (listed as *P. sp. aff. latistipula* in Cheek et al. 2004), *Rhaptopetalum geophylax* Cheek & Gosline, *Sabicea* sp. nov. (listed as *Sabicea* sp. A in Cheek et al. 2004) and *Talbotiella bakossiensis* Cheek. It is likely that more 'Kupe-Bakossi endemics' will be discovered in Rumpi, especially since parts of the chain are still unexplored. In addition, there is at least one species, *Ocotea ikonyokpe* van der Werff, which is only known from Rumpi. The Rumpi Hills are therefore a priority site for plant conservation. Although the lower areas have mostly been cleared, submontane forest above c. 1100 m is still largely intact. The site is so far protected only as a forest reserve, and an upgrading of its status should be considered, especially since, in addition to its very rich flora, it also holds most of the Cameroon highlands endemic birds, and is considered an Important Bird Area (BirdLife International 2009).

Tchabal Mbabo (2460 m) is a mountain situated in the savanna zone, but which has an outlier of montane forest, the northernmost spot of this forest type in Cameroon. It is hardly known botanically, apart from collections by Jacques-Félix dating back to the 1930s. We only briefly visited the site but discovered there a new species of *Impatiens* and a new population of the threatened *Oxyanthus okuensis*, hith-

erto only known from the Oku area. The forests of Tchabal Mbabo appear quite similar floristically to those of Oku, so further discoveries may be expected there.

One would hesitate to qualify the Yaoundé area as little-known, considering the large number of botanists that have collected there. However, it appears that the rocky hills surrounding the city have not received due attention. A remarkable illustration of this situation is the discovery of *Psychotria yaoundensis* which, although growing in the city's immediate outskirts, escaped the attention of collectors until 2009. These rocky hills, mostly 800–1100 m in altitude, have a very interesting flora with several endemic or extremely rare species, e.g. *Afrothismia amietii* Cheek, *Pristimera breteleri* N.Hallé, *Talbotiella breteleri* (Aubrév.) Mackinder & Wieringa and *Multidentia saxicola* O.Lachenaud & Séné (the latter also known from one locality in D.R.Congo). Unfortunately these species are now severely threatened as the city is expanding in a rather anarchic way, with houses being built even on fairly steep slopes. Yet, although exploration and conservation efforts are probably more urgent there than anywhere else in the country, there have been very little if any in recent years. We strongly recommend further inventories to be carried out in the area, in order to identify priority sites for conservation.

The Mbam-Minkom massif, although part of the same formation as the other hills around Yaoundé, stands apart in its higher altitude (1295 m) which allows the presence of submontane forest on the summit. Interestingly this submontane forest has some affinities with the Western Cameroon highlands, as shown by the occurrence of extralimital populations of *Chassalia laikomensis* and *Mussaenda epiphytica*. Mbam-Minkom is also home to the endemic *Coffea fotsoana* Stoffelen & Sonké, and several interesting orchids have been recorded there (Droissart et al. 2009a, Simo et al. 2009). The area is unprotected and deforestation is ongoing on the lower slopes. This is unfortunate since the site, beside its floristic interest, has a strong touristic potential, due to its beautiful landscape, the presence of two emblematic and highly threatened animal species (the gorilla and the grey-necked picathartes), and the vicinity of Yaoundé.

There are further areas in Cameroon which definitely need better botanical prospecting. These include the Nta Ali massif near Mamfe, the hilly area between Yabassi and Ndi-kiniméki, and the Mambe hills between Edea and Yaoundé, all of which have only been briefly visited by botanists. The extreme southeast (i.e. east of the Dja reserve) is also little-known. The few botanical expeditions there have mostly followed the main roads and watercourses, leaving aside the more hilly areas near the Congo border. The forests of the Adamaoua have also received little attention. They are evidently not as diverse as those in the south of the country, but nevertheless have some species found nowhere else in Cameroon, e.g. *Sericanthe raynaliorum* (N.Hallé) Robbr. Finally, large parts of the savanna region have not or scarcely been explored, and would certainly yield a number of additions to the country's flora.

ACKNOWLEDGEMENTS

The new species here described was discovered in the company of Olivier Sounigo and Régis Babin of CIRAD, Yaoundé, who first drew our attention to the Nkolbisson hills. The first author is a research fellow of the F.R.S.-F.N.R.S. (National Fund for Scientific Research). This institution, as well as the F.F.R.S.A. (Fondation pour Favoriser les Recherches Scientifiques en Afrique) supported our research in Cameroon. We thank the Cameroonian authorities for permitting our research. Stévant's participation was supported by the U.S. National Science Foundation (1051547, TS as PI). We are particularly grateful to the National Herbarium of Cameroon, and its Director Dr Jean-Michel Onana, for their collaboration. The herbarium staff of Hamburg, Kew, Paris, and Wageningen are thanked for their assistance while working there, and for sending specimens on loan. We would also like to acknowledge the Sud Expert Plantes project under French Ministry of Foreign Affairs, for providing financial support for the fieldwork.

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Manuscript received 11 Jan. 2011; accepted in revised version 11 Oct. 2012. This paper was pre-published on 20 Mar. 2013 in issue 146(1) of *Plant Ecology and Evolution*.

Communicating Editor: Elmar Robbrecht.

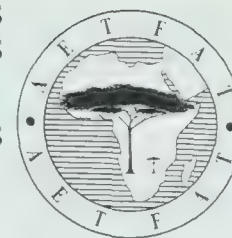
Note added to reprint version:

The second to last sentence of the Discussion should read:

“They are evidently not as diverse as those in the south of the country, but nevertheless have some species found nowhere else in Cameroon, e.g. *Sericanthe raynaliorum* (N.Hallé) Robbr. (Sonké et al. 2012).”

Reference:

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The endemic and non-endemic vascular flora of Madagascar updated

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Background and aims – The *Catalogue of the Vascular Plants of Madagascar* project aims to evaluate and enumerate the native and naturalized vascular plant flora of Madagascar. In light of the past two decades of intensive collecting and taxonomic work, all relevant published literature and available specimens are being reassessed in order to evaluate the taxonomic status and distribution of the native and naturalized taxa of vascular plants. Here we provide current figures for the total numbers of vascular plants and levels of endemism at the order, family, genus and species levels, comparing them to previous historical counts and analyzing the distribution of the non-endemic element of the flora.

Key Results – At the time of writing (April 2010), more than a century after Baron first counted 4,100 species of vascular plants in Madagascar, the *Madagascar Catalogue* database had registered a total of 14,883 accepted names at all taxonomic levels (64 orders, 243 families, 1,730 genera, 11,220 species and 1,626 infraspecific taxa). Of the 11,220 species of vascular plants in Madagascar, 10,650 (95%) are angiosperms, of which 331 are naturalized introduced species. The remaining accepted indigenous angiosperm species total 10,319, of which 8,621 (84%) are endemic to Madagascar (82% endemism for all indigenous vascular plants). Among the 1,698 non-endemic species of indigenous angiosperms, a total of 1,372 (81%) also occur in Africa, of these 654 (39%) are present only in Africa and Madagascar.

Key words – Endemism, flora, Madagascar, non-endemism.

"It may now be said with perfect truth that the vegetable productions of Madagascar have been, though not thoroughly, very extensively explored, and that the majority of the plants inhabiting the island are known to science."

Rev. Richard Baron, 1 November 1888.

INTRODUCTION

The island of Madagascar is renowned for its exceptional biodiversity, with extraordinary levels of species diversity and endemism, a consequence of over 100 million years of evolution in relative isolation (Goodman & Benstead 2005). At the center of that biodiversity is a flora unparalleled in its diversity and distinctiveness. However, despite more than two centuries of botanical exploration, the inventory, description, and documentation of the Malagasy flora are still far from complete.

In 2003, the Missouri Botanical Garden commenced development of a dedicated on-line resource for the dissemination of detailed information on the vascular plant flora of Madagascar. The *Catalogue of the Vascular Plants of Madagascar* represents an analysis and evaluation of the current status of the taxonomy of every vascular plant genus based both on the published literature and the examination of all available specimens. The resulting database enumerates all accepted indigenous and naturalized species present in Madagascar and their synonyms, and provides estimates of the number of undescribed species in each genus. The information is presented as a freely available, on-line, browsable and searchable database (<http://www.efloras.org/madagascar>) that includes nomenclatural data, verified representative specimen data, type and specimen-vouchered living plant images, maps, vernacular names and conservation status. The data derive in part from the *Flore de Madagascar et des Comores* series, published by the Paris Museum, which has

so far treated 165 of the 222 (74%) traditionally recognized plant families in Madagascar, which amount to approximately 6,500 species (Phillipson et al. 2006). The first volume, treating Aponogetonaceae, appeared in 1936, and most of the subsequent volumes were published during the following thirty years. Full or partial taxonomic treatments for genera in some of the remaining families have been published elsewhere (notably in the journal *Adansonia*), and some excellent detailed monographs, such as for the legumes (Du Puy et al. 2002) and palms (Dransfield & Beentje 1995) are available. Our knowledge of the flora of Madagascar is thus advancing steadily. However, many of the treatments in earlier volumes are now badly outdated and are of little use today, and some families/genera have never been treated. For many groups there thus remains an urgent need for taxonomic revision.

Moreover, to reconcile nomenclatural inconsistencies among the taxa shared between Africa and Madagascar, and thereby to render more comprehensive their synonymy, during the past year we have brought core *Madagascar Catalogue* data into the *African Plants Database* developed by the Conservatoire et Jardin botaniques de la Ville de Genève and the South African National Biodiversity Institute in Pretoria (<http://www.ville-ge.ch/cjb/bd/africa/>). The combined databases now extend the scope of the APD nomenclatural index to include all taxa present in continental Africa and Madagascar.

Although Madagascar has been widely recognized for many years as a unique centre of diversity and endemism, until now precise figures for the flora have not been available (Morat & Lowry 1997). Based on the *Madagascar Catalogue*, we present here: (1) a current estimate of the total numbers of indigenous and naturalized vascular plant taxa in Madagascar; (2) updated figures for the levels of endemism at the family, genus and species level, as well as an analysis of the distribution of the non-endemic element of the flora; and (3) a discussion of the updated figures for diversity and endemism in the context of the historical progression of our knowledge on the flora of Madagascar during the course of the 20th and start of the 21st century.

RESULTS

Diversity, endemism and non-endemism

As of April 2010 the *Madagascar Catalogue* database had registered a total of 14,883 accepted names at all taxonomic levels, the ranks of family and above following the most recent Angiosperm Phylogeny Group classification (APG III 2009), comprising: 64 orders, 243 families, 1,730 genera, 11,220 species and 1,626 infraspecific taxa (392 subspecies, 1,137 varieties and 97 forms) (table 1). Pteridophyte data are not yet complete, but a recent account by Rakotondrainibe (2003) enumerated a total of 586 species (265 endemic species, 45%) in Madagascar, of which 563 species are currently incorporated into the *Madagascar Catalogue* (257 endemic species, 46%). The gymnosperms are represented in Madagascar by only seven species: six in the genus *Podocarpus* L'Hér. ex Pers. (all endemic) and a native non-endemic species of *Cycas* L. (*C. thouarsii* Gaudich).

Table 1 – Actual figure of the Malagasy flora.
Pterido. = Pteridophytes; Gymno. = Gymnosperms; Angio. Angiosperms.

	Pterido.	Gymno.	Angio.	total
orders	15	2	47	64
families	29	2	212	243
genera	107	2	1,621	1,730
species	563	7	10,650	11,220
subspecies	0	0	392	392
varieties	39	5	1,093	1,137
forms	0	0	97	97

Five families are endemic to Madagascar: Asteropeiaceae, Barbeuiaceae, Physenaceae, Sarcolaenaceae and Sphaerosepalaceae. Currently, Orchidaceae are the family with the largest number of species (862 species), followed by Rubiaceae (660 species) and Fabaceae (592 species). Among the families that contain only endemic species, the more diverse are the Balsaminaceae (one genus, *Impatiens* L. with 173 species), Pandanaceae (two genera, *Martellidendron* Callm. & Chassot [five species] and *Pandanus* Parkinson [84 species]) and Bignoniaceae (eleven genera and 75 species). The latter family is currently being revised by MWC and PBP, and is expected to exceed 100 endemic species.

A total of 1,730 vascular plant genera containing indigenous species are known from Madagascar, of which 321 (19%) are endemic. Among the endemic genera, the most species rich are *Aspidostemon* Rohwer & H.G.Richt. (Lau-

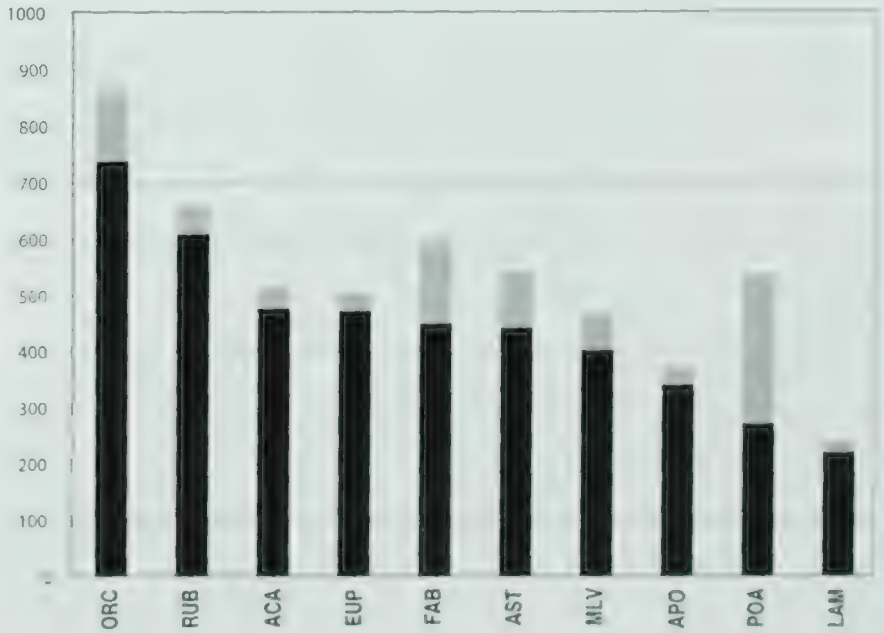


Figure 1 – The ten families with the largest number of endemic species in the Malagasy native angiosperm flora. Black, endemic species; grey, non-endemic species. ORC: Orchidaceae (862 species: 737 E [85%], 125 NE); RUB: Rubiaceae (660 species: 608 E [92%], 52 NE); ACA: Acanthaceae (512 species: 476 E [93%], 36 NE); EUP: Euphorbiaceae (504 species: 473 E [94%], 31 NE); FAB: Fabaceae (592 species: 449 E [76%], 125 NE); AST: Asteraceae (540 species: 441 E [88%], 99 NE); MLV: Malvaceae (466 species: 402 E [86%], 64 NE); APO: Apocynaceae (371 species: 339 E [91%], 32 NE); POA: Poaceae (536 species: 271 E [51%], 265 NE); LAM: Lamiaceae (240 species: 219 E [91%], 21 NE). Families' acronyms following Weber (1982)

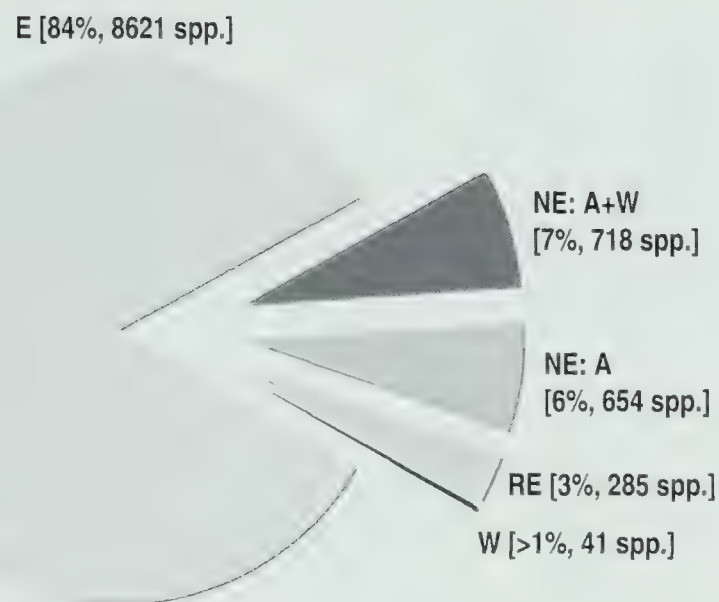


Figure 2 – Endemism and non-endemism in the Malagasy native angiosperm flora; E, Endemic; NE, Non-Endemic; RE, Regional Endemic; A, Africa; W, World (extra-Africa).

raceae) and *Microsteira* Baker (Malpighiaceae) (each with 28 species), followed by *Capurodendron* Aubrév. (Sapotaceae) (23 species), *Schizolaena* Thouars (Sarcolaenaceae) (twenty species) and *Rhopalocarpus* Bojer (Sphaerosepalaceae) (seventeen species). Among the endemic genera, 139 (43%) are monotypic and 87 (27%) have only two or three species. Several of the monotypic genera are illustrative of the biogeographically unique Malagasy flora, such as *Humbertia* Lam. (Convolvulaceae), the basal genus sister to the rest of the family (Stefanović et al. 2002) and formerly placed in a family on its own; *Barbeuia* Thouars, the sole genus of Barbeuiaceae, an isolated family within the order Caryophyllales (Cuénoud et al. 2002); *Diegodendron* Capuron (Bixaceae), sister to the Neotropical genus *Bixa* L. (Bayer et al. 1999), formerly recognized as an endemic family Diegodendraceae; *Malagasiasia* L.A.S. Johnson & B.G. Briggs (Proteaceae), sister to the monotypic Australian genus *Catalepidia* P.H. Weston (Weston & Barker 2006), and *Takhtajania* Baranova & J.-F. Leroy (Winteraceae), an emblematic basal genus that likely dates to the upper Cretaceous (84 mya) (Marquinez et al. 2009).

Currently, the *Madagascar Catalogue* lists 10,889 accepted vascular plant species indigenous to Madagascar (i.e. excluding naturalized species), of which 8,884 (82%) are endemic to Madagascar, and thus 2,005 (18%) species (1,698 angiosperms) are native but non-endemic. More than 50% of the endemic flora is concentrated in ten families (fig. 1). Among the non-endemic species, their global distribution range most frequently includes part of continental Africa. A total of 1,372 angiosperm species (81% of the angiosperm non-endemic species) are shared with Africa, of which 654 species are present only in Africa and Madagascar (fig. 2). The remaining non-endemic species are shared among the nearby western Indian Ocean islands (Comoros, Mascarenes, and Seychelles) (285 species) and Asia and/or the New World (41 species). The distribution of the 285 species shared with the regional islands is shown in figure 3. The 143 species shared only with the Comores belong to 46 families, of which 31 are represented by only one or two species; the three families with the most species are Orchidaceae (34 species), Fabaceae (eight species) and Poaceae (seven species). The ninety spe-

cies shared only with the Mascarenes belong to 31 families, of which fifteen are represented by only one or two species; the three families with the most species are Orchidaceae (thirty species), Rubiaceae (seven species) and Myrtaceae (four species). It is interesting to note that Orchidaceae with their minute seeds have the highest number of angiosperm species shared with the western Indian Ocean islands. Recent molecular phylogenetic studies have revealed the relationships and patterns of speciation among Orchidaceae of the Mascarenes with respect to Madagascar (Micheneau et al. 2008).

Below the species level, the *Madagascar Catalogue* lists many infraspecific taxa on a provisional basis only, since further systematic studies are generally required to evaluate whether they merit recognition, and if so, at what taxonomic level.

Current figures in comparison to historical counts

With great confidence, the Rev. Richard Baron announced the first count for the vascular flora of Madagascar before the Linnaean Society on 1 Nov. 1888, citing 4,100 indigenous species, of which about 3,000 (73%) were endemic (Baron 1889). He then compiled the first comprehensive list of taxa in the *Compendium des Plantes Malgaches* (1900–1906), enumerating over 4,700 species and varieties amongst 970 genera (Dorr 1987). Perrier de la Bâthie intended to continue Baron's *Compendium* through the serial publication of a *Catalogue des plantes de Madagascar* (1930–1940); in his 1936 *Biogéographie des Plantes de Madagascar*, Perrier de la Bâthie counted 6,765 native species (out of a total flora of 7,370) of which 5,820 (86%) were considered to be endemic. More than twenty years later, Humbert (1959) enumerated 7,900 species, 81% of which he considered to be endemic, and estimated that the eventual total would reach 10,000 species. Koechlin et al. (1974) then increased the enumeration to 8,500 species without reconsidering the level of endemism and estimated a total number of vascular plants at 10,000–12,000 species, the latter figure following the estimate of DeJardin et al. (1973). Phillipson (1994) incorporated the c. 1,170 endemic species described between 1959 and 1992, as well as a proportional estimate of new records of non-endemic species, to arrive at a total of 9,345 species

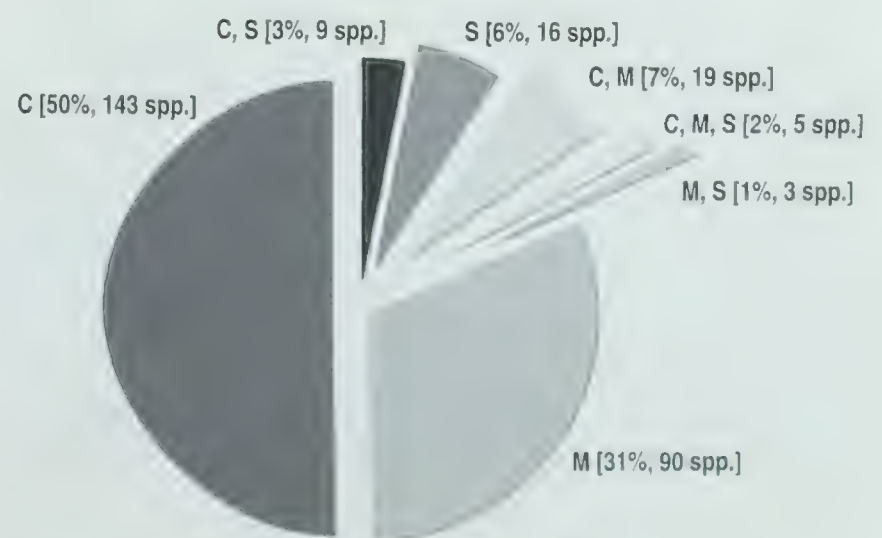


Figure 3 – Distribution of the non-endemic Malagasy species shared only with the regional western Indian Ocean islands; C, Comores islands; S, Seychelles islands; M, Mascarenes islands.

Table 2 – Historical progression of knowledge on the Malagasy flora.

1889, Baron; 1900–1906, Baron’s *Compendium* (Dorr 1987); 1936, Perrier de la Bâthie; 1959, Humbert; 1974, Koechlin et al.; 1994, Phillipson; 2010, *Madagascar Catalogue* (square brackets refer to angiosperms only). Nat., naturalized; NE, Non Endemic; E, Endemic; *not including Pteridophytes; ** not known for naturalized species.

Years	1889	1900–1906	1936	1959	1974	1994	2010
Families	-	-	191	183	207	-	243
Genera	-	970	1289	1280*	1382	-	1730
Species	4100	4700	7370	7900	8500	9345	11220
Pterido.	-	-	505	550	550	-	563
Gymno.	-	-	3	5	5	-	7
Angio.	-	-	6862	7345	7945	-	10650
Genera							
Nat.	-	-	150	1040**(81%)	-	-	113
Native NE	-	-	901 (79%)	-	-	-	1296 (80%)
E	-	-	238 (21%)	240 (19%)	-	-	321 (20%)
Species							
Nat.	-	-	605	1500** (19%)	-	-	331
Native NE	-	-	945 (14%)	-	-	-	2005 [1698] (18%)
E	3000 (73%)	-	5820 (86%)	6400 (81%)	-	7570 (81%)	8884 [8621] (82%)

(with 7,570 endemic) (table 2). The present *Madagascar Catalogue Project* represents the first effort since Perrier de la Bâthie (1930–1940) to list all of the vascular plant species indigenous or naturalized in Madagascar, and with the current figure of 11,220 vascular plant species, we are now approaching the highest earlier estimate of 12,000 species (table 2). With regard to the level of native species endemism, the current figure of 82% (84% for angiosperms only) is close to the 83% reported by Goodman & Benstead (2005) for a subset of c. 3,000 species that included the ferns (only 45% endemism). When the current *Madagascar Catalogue* database is partitioned by habit, species endemism for trees and shrubs combined reaches 92%, which compares to the 96% endemism figure reported by Schatz (2001) for a subset of 4,220 trees and large shrubs. The level of endemism for herbs is only 72%, reflecting again the much lower levels of endemism in the predominantly herbaceous large families Poaceae (536 species, 51% endemic) and Cyperaceae (304 species, 39% endemic). Since the *Madagascar Catalogue Project* reviews each genus and provides an estimate of the number of undescribed species (nearly all of which will be endemic), we can extrapolate based on those genera for which full evaluations have been completed. This allows us to provide new estimates for both the total number of indigenous and naturalized plant species in Madagascar as well as the true level of species endemism among the indigenous flora (Phillipson et al. in prep.). Both figures appear to be converging on the estimates of Phillipson et al. (2006) of 14,000 species of indigenous and naturalized plants and 85% indigenous species endemism, confirming Madagascar’s critical role in harbouring a unique and globally important assemblage of plants.

ACKNOWLEDGMENTS

We are grateful to the XIXth AETFAT Congress Committee, especially the Secretaries General, Vololoniaina Jeannoda

(Département de Biologie et Ecologie végétales, Université d’Antananarivo, Madagascar) and Sylvain Razafimandimbison (The Bergius Foundation, Royal Swedish Academy of Sciences, Sweden). We thank the staffs of the Missouri Botanical Garden in St. Louis and Antananarivo, the Conservatoire et Jardin Botaniques de la Ville de Genève (especially Pierre-André Loizeau and Markus Fischer) and at the Muséum National d’Histoire Naturelle de Paris. We also thank Roy Gereau and Henk Beentje for helpful comments on an earlier version of the manuscript. Finally, we are grateful to the many generations of botanists whose hard work and dedication have contributed to building our knowledge of the Malagasy flora. Financial support was provided by grants from the U.S. National Science Foundation (0743355), the Andrew W. Mellon Foundation, the J.R.S. Biodiversity Foundation and Krukoff Fund for African Botany.

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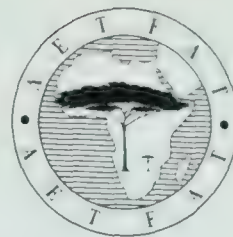
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Manuscript received 25 Aug. 2010; accepted in revised version 19 Nov. 2010. This paper was pre-published on 15 Jun. 2011 in issue 144(2) of *Plant Ecology and Evolution*.

Communicating Editor: Sylvain Razafimandimbison.



Richness, similarity and specificity of Madagascar flora compared with Sub-Saharan Africa

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Background and aims – Based on presence/absence information for all angiosperms in Tropical Africa, Southern Africa and Madagascar, we review the similarities and differences between these floras. We compare specific and generic richness for the three areas, and examine their degree of overlap. Madagascar and Sub-Saharan Africa are compared in terms of: the specific and generic richness of their angiosperm families, and specific richness of their genera.

Methods – Using the *African Plant Database*, global figures of specific and generic richness for Tropical Africa, Southern Africa and Madagascar have been calculated and illustrated by Venn diagrams. For each family or genus similarity between Sub-Saharan Africa and Madagascar has been calculated using the Jaccard Index. Madagascar specificity has been defined as the ratio of Madagascar-exclusive species richness to total richness.

Key results – The study confirms the general trends of richness and endemism in the Malagasy flora, but provides accurate figures based on the current state of angiosperm taxonomy. Overlap between the floras of Southern African, Tropical African and Madagascar flora is provided with precise figures. Similarity between Madagascar and Sub-Saharan Africa is very low at species level (0.029) and eight times higher at generic level (0.246). Madagascar specificity reaches 0.165 at specific level and 0.105 at generic level. Calculation of these two indexes for families and genera, based for the first time on APG III, confirms general trends observed so far, and the richest families of the Malagasy flora are listed according to major patterns of their diversity and distribution.

Key words – Madagascar, Africa, African Plant Database, biogeography, diversity, specific and generic richness, similarity, specificity.

INTRODUCTION

Intuitively, it has always been assumed that the biogeographic connections of the living organisms of Madagascar are primarily with Africa – the Mozambique Channel being no more than 400 km broad at its narrowest point. In Engler's (1882) classical phytogeographic system, Madagascar is considered to be part of the Paleotropical Floristic Kingdom, included within its African Territory. Although, as Engler pointed out, some elements are shared with tropical Asia (his "Monsoon Territory"). Following this early work, these main trends have been confirmed by numerous botanists in works focusing on the Malagasy flora (Baron 1889, Hochreutiner 1907, Perrier de la Bâthie 1936, Humbert 1959, Leroy 1978),

while the Asian connections were specifically reviewed more recently by Schatz (1996).

Recent developments in continental checklists have allowed the compilation of a database that includes all angiosperm species in Africa and Madagascar. Analysis of this unique data set provides accurate figures for the first time on the richness and degree of overlap of these floras based on the entire angiosperm flora. In a separate contribution, the authors have proved statistics for the endemism of the Malagasy flora based on a revised dataset for Madagascar (Callmander et al. 2011). Here, however, we concentrate on the richness, similarity and specificity of the Malagasy flora, as compared to the continental Sub-Saharan Africa.

METHODS

The *African Plant Database* (<http://www.ville-ge.ch/cjb/bd/africa/>) has developed since 2002 through the collaboration between the South African National Botanical Institute and the Conservatoire et Jardin botaniques de la Ville de Genève (Gautier et al. 2006). The merging of checklists for Tropical Africa (Lebrun & Stork 1991–1997) and Southern Africa (Germishuisen & Meyer 2003) has resulted in the first consolidated checklist of all angiosperm species for Sub-Saharan Africa (Klopper et al. 2006). The database developed further in 2007 with the incorporation of a set of North African data provided by Alain Dobignard (Dobignard & Chatelain 2010–2011) and subsequently floristic information for Madagascar have been integrated through collaboration with Missouri Botanical Garden, and the *Catalogue of the Vascular Plants of Madagascar Project* (<http://www.efloras.org/madagascar>). In its current state, the *African Plant Database* (APD) represents a unique source of information on angiosperms for the continental Africa and Madagascar, providing a synonymy index and nomenclatural information for more than 187,500 names, as well as information on the ecology and geographic distribution of the c. 63,500 accepted species of the area. However, data on the other Indian Ocean Islands (Mascarenes, Comoros and Seychelles) have not yet been included. The systematic screening of published botanical literature enables the incorporation of new information and we envisage this to continue for the foreseeable future thus providing a permanently updated database.

APD will continue to evolve as new information becomes available and taxonomic changes are incorporated from different sources, and it is important to mention that the data analyzed for this present article were extracted from the database in April 2011. This accounts for small discrepancies in some of the statistics on endemism provided here for Madagascar as compared with our analysis of updated information from the Madagascar Catalogue in our related article (Callmander et al. 2011). For analyses, a taxon is considered present in an area if it is native to the area.

Our preliminary analysis of the data in the APD indicated that there were only 371 species shared between North Africa and Madagascar, representing less than 0.6% of total, and being generally widely dispersed cosmopolitan species, like *Amaranthus viridis* L., *Waltheria indica* L. or *Corchorus tridens* L. (nomenclature follows APD). Only eighteen species (mainly naturalized cultivated temperate plants) were shared between Madagascar and North Africa only. As a consequence, data from APD have first been filtered to eliminate all records of taxa occurring North of the Sahara for the analyses presented here.

Based on species distribution information in the APD, we classified each species and genus according to their presence in:

Madagascar (MA)

Southern Africa (SA) (including RSA, Namibia, Botswana, Lesotho, and Swaziland)

Tropical Africa (TA) (i.e. Sub-Saharan Africa, but excluding the preceding)

Venn diagrams were then drawn to illustrate the extent of overlap imbrications of the floras at specific and generic levels.

In a second analysis, data from SA and TA were grouped as Sub-Saharan Africa (SSA). Each species was assigned to one of the following categories:

MA endemic

MA non-endemic, but absent from SSA

present both in MA and in SSA (and possibly elsewhere)

absent from MA, present in SSA (and possibly elsewhere)

These data were then grouped as follows to allow analyses at three different levels: specific richness per family, generic richness per family, and specific richness per genus. Attribution of genera to families follows APG III (APG 2009). At each level of analysis, similarity and specificity of Madagascar relative to SSA was calculated. For similarity we used the Jaccard Index, i.e. the ratio of the number of shared species (or genera) to total richness (Jaccard 1901). Madagascar specificity is defined here as the ratio of the number of Madagascar species (or genera) absent from SSA to total richness. For each of these analyses, a global value (i.e. for the whole angiosperm flora) was calculated, as well as value for each taxon considered. The value is considered as high if it is more than 3/2 times the global value. It is considered as low if it is less than 2/3 the global value.

RESULTS

Comparison of the specific and generic richness between Tropical Africa (TA), Southern Africa (SA) and Madagascar (MA)

Total specific richness for the area comprises 55,099 species. A Venn diagram of specific richness for the three areas is shown in fig. 1. With 29,833 species (54.1% of total) TA is the richest, followed by SA: 20,617 (37.4%) and MA: 10,657 (19.3%). Only 817 species (1.5%) are shared among all three areas. The overlap between TA and SA (but excluding MA) is high, with 3,613 species. It is c. five times greater

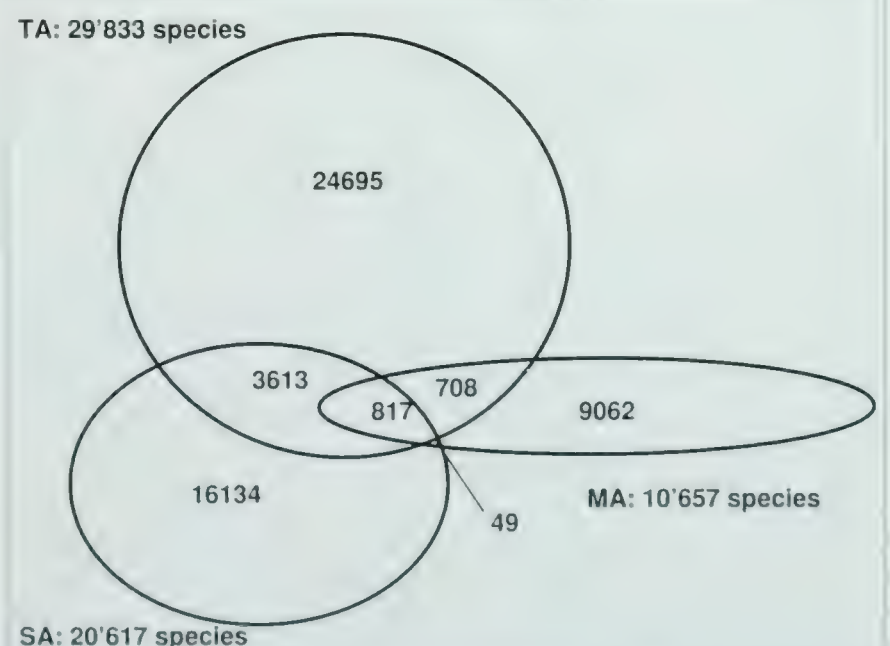


Figure 1 – Venn diagram of specific richness in Tropical Africa (TA), Southern Africa (SA) and Madagascar (MA).

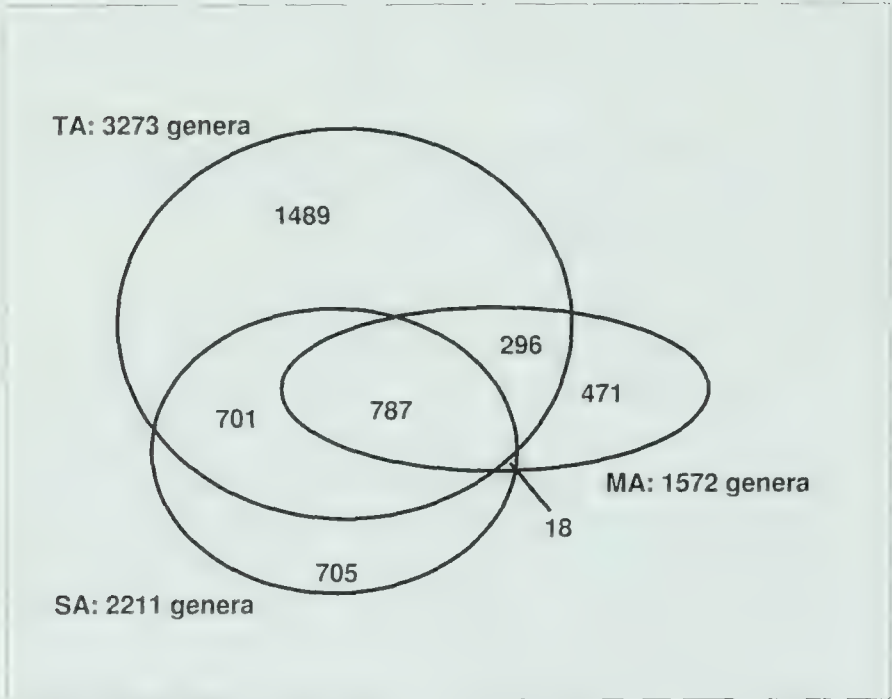


Figure 2 – Venn diagram of generic richness in Tropical Africa (TA), Southern Africa (SA) and Madagascar (MA).

than the overlap between TA and MA (excluding SA), which totals only 708. Only 49 species are shared uniquely between SA and MA.

At generic level (fig. 2), total richness is 4467 genera, with the same ranking of the 3 areas: TA: 3273 genera (73.3% of total), SA: 2211 (49.5%); MA: 1572 (35.2%). Overlap of generic richness is of course higher than at specific level: 787 genera (17.6%) are shared amongst all three regions, which represents a 12-fold percentage increase compared to specific level. The proportion of genera which occur in two regions only is also higher than at species level. Compared with species level it increases by 2.4-fold between TA and SA only, but by more than 4.5-fold for both TA-MA and SA-MA. Consequently, the percentage of genera limited

to one of the three regions decreases compared with specific level, especially for SA and MA.

Comparison of the specific richness of families between Madagascar (MA) and Sub Saharan Africa (SSA)

Table 1 presents specific richness, MA–SSA similarity and MA specificity for the thirty most species-rich families in Madagascar.

The five richest families in Madagascar are the same as for the whole area, but in a different sequence. Orchidaceae rank first in MA, but are only fourth for the whole area, for which Fabaceae, Asteraceae and Rubiaceae are first, second and third respectively. Other families which increase significantly their richness ranking in MA compared to total area include: Melastomataceae; Arecaceae; Balsaminaceae; Lauraceae; Primulaceae; Sapindaceae, Salicaceae, Pandanaceae and Ebenaceae. Conversely: Aizoaceae, Iridaceae, Asparagaceae, Proteaceae and Geraniaceae (all families highly represented in the Cape Floristic Region) have a significantly lower rank for MA than for total area.

The global value for similarity between MA and SSA, based on the Jaccard index is very low (0.029). Notable exceptions ($> 1.5 \times$ global value) include Poaceae, Cyperaceae and Convolvulaceae. On the contrary, low values ($< 2/3 \times$ global value) occur in many of these top 30 families in Madagascar: notably in Pandanaceae, Bignoniaceae and Malpighiaceae, which have no species in common between the two areas, but also in Annonaceae, Xanthorrhoeaceae, Sapotaceae, Balsaminaceae, Lauraceae, Ebenaceae, Euphorbiaceae, etc.

Madagascar specificity (see also fig. 3A & B) has a global value of 0.165. It is especially high ($> 1.5 \times$ global value) in eighteen of these thirty families notably in Arecaceae, Pandanaceae, Malpighiaceae, Balsaminaceae, Lauraceae, Bigno-

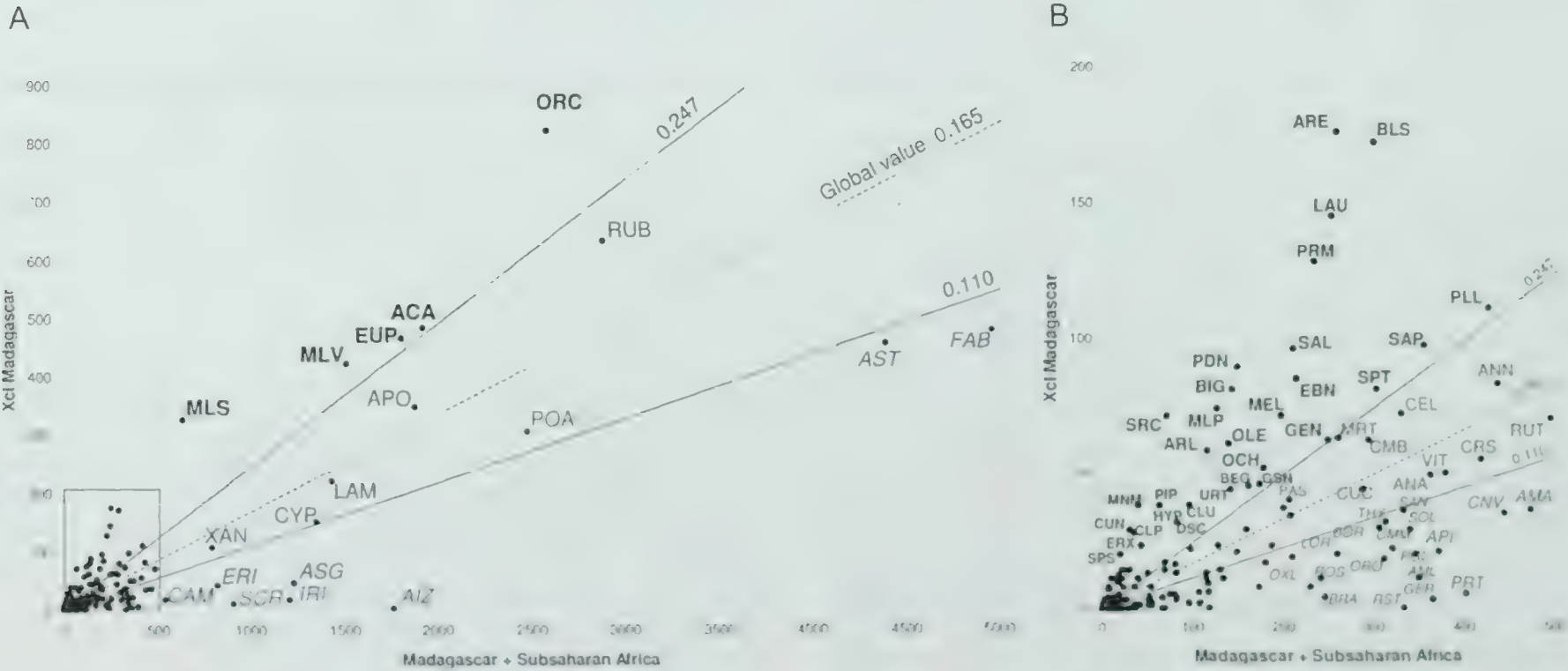


Figure 3 Specific richness of families. X-axis: number of species in the whole area (Sub Saharan Africa and Madagascar); Y-axis: number of species occurring only in Madagascar (and possibly elsewhere, but not in SSA). Dotted line: global value for all angiosperms. Solid lines: 0.110 ($2/3 \times$ global value) and 0.247 ($1.5 \times$ global value) ratios. Acronyms of families according to Weber (1982) Italics and bold: Families with low (resp. high) Madagascar specificity. A, whole graph; B, detail of bottom-left corner.

Table 1 – Species richness, similarity and Madagascar specificity of the top 30 species-rich families in Madagascar.
Xcl: exclusively; end: endemics; MA: Madagascar; SAA: Sub Saharan Africa; high values ($> 1.5 \times$ global value) of affinity and specificity in bold, low values ($< 2/3 \times$ global value) in italics.

Family	Total MA	Xcl MA (end MA)	Total SSA	Xcl SSA	Shared MA / SSA	Total	Similarity	Specificity
Orchidaceae	869	821 (734)	1761	1713	48	2582	<i>0.019</i>	0.318
Rubiaceae	675	631 (612)	2247	2203	44	2878	<i>0.015</i>	0.219
Fabaceae	640	478 (449)	4479	4317	162	4957	0.033	<i>0.096</i>
Poaceae	566	306 (272)	2176	1916	260	2482	0.105	0.123
Asteraceae	541	455 (441)	3935	3849	86	4390	0.020	<i>0.104</i>
Acanthaceae	512	484 (476)	1437	1409	28	1921	<i>0.015</i>	0.252
Malvaceae	486	424 (402)	1090	1028	62	1514	0.041	0.280
Euphorbiaceae	484	467 (448)	1339	1322	17	1806	<i>0.009</i>	0.259
Apocynaceae	376	349 (336)	1532	1505	27	1881	<i>0.014</i>	0.186
Melastomataceae	335	328 (325)	313	306	7	641	<i>0.011</i>	0.512
Cyperaceae	287	152 (120)	1203	1068	135	1355	0.100	0.112
Lamiaceae	249	222 (218)	1214	1187	27	1436	<i>0.019</i>	0.155
Arecaceae	181	176 (175)	80	75	5	256	0.020	0.688
Balsaminaceae	173	172 (172)	125	124	1	297	<i>0.003</i>	0.579
Lauraceae	146	145 (142)	106	105	1	251	<i>0.004</i>	0.578
Primulaceae	133	128 (122)	104	99	5	232	0.022	0.552
Phyllanthaceae	122	111 (100)	313	302	11	424	0.026	0.262
Xanthorrhoeaceae	110	108 (108)	690	688	2	798	<i>0.003</i>	0.135
Sapindaceae	106	97 (93)	257	248	9	354	0.025	0.274
Salicaceae	99	96 (96)	114	111	3	210	<i>0.014</i>	0.457
Convolvulaceae	90	35 (30)	408	353	55	443	0.124	<i>0.079</i>
Pandanaceae	89	89 (89)	60	60	0	149	<i>0.000</i>	0.597
Ebenaceae	86	85 (84)	129	128	1	214	<i>0.005</i>	0.397
Celastraceae	84	72 (71)	257	245	12	329	0.036	0.219
Annonaceae	84	83 (80)	352	351	1	435	<i>0.002</i>	0.191
Sapotaceae	82	81 (79)	221	220	1	302	<i>0.003</i>	0.268
Bignoniaceae	81	81 (79)	62	62	0	143	<i>0.000</i>	0.566
Rutaceae	75	70 (65)	424	419	5	494	<i>0.010</i>	0.142
Malpighiaceae	74	74 (74)	52	52	0	126	<i>0.000</i>	0.587
Meliaceae	74	71 (68)	126	123	3	197	<i>0.015</i>	0.360
...	...		...	...	...	...	...	...
Total	10657	9083 (8583)	46016	44442	1574	55099		
Global value							0.029	0.165

niaceae, Primulaceae and Melastomataceae. Low values ($< 2/3 \times$ global value) were obtained for Convolvulaceae, Fabaceae, and Asteraceae. Others major families (> 400 species in total area) with a low MA specificity include Aizoaceae, Asparagaceae, Iridaceae, Scrophulariaceae, Ericaceae, Campanulaceae, Amaranthaceae and Proteaceae, which are relatively poor in species richness in MA.

Comparison of the generic richness of families between Madagascar (MA) and Sub Saharan Africa (SSA)

Table 2 presents generic richness, MA–SAA similarity and MA specificity of the 38 families with ten or more genera in Madagascar.

The nine richest families for genera are the same as for species, although their sequence differs slightly. Compared with total area, Poaceae rank first in MA, but third globally, these ranks being inverted for Asteraceae. As a whole, there is much less difference in generic richness ranking between MA and the total area than for specific richness ranking. However some families display a higher rank of generic richness for the whole area. These include predominantly subtropical-temperate families like Brassicaceae, Aizoaceae, Iridaceae, Scrophulariaceae, Caryophyllaceae and Apiaceae, but also some predominantly tropical families like Annonaceae, Sapotaceae and Rutaceae. On contrary some families have a higher rank in MA like Sarcolaenaceae (MA endemic

Table 2 – Generic richness, similarity and Madagascar specificity of the top 38 genus-rich families in Madagascar.
Xcl: exclusively; end: endemics; MA: Madagascar; SAA: Sub Saharan Africa; high values ($> 1.5 \times$ global value) of affinity and specificity in bold, low values ($< 2/3 \times$ global value) in italics.

Family	Total MA	Xcl MA	Total SSA	Xcl SSA	Shared MA / SSA	Total	Similarity	Specificity
Poaceae	143	25	305	187	118	330	0.358	0.076
Fabaceae	112	27	316	231	85	343	0.248	0.079
Asteraceae	100	26	355	281	74	381	0.194	<i>0.068</i>
Rubiaceae	88	38	197	147	50	235	0.213	0.162
Acanthaceae	66	30	86	50	36	116	0.310	0.259
Orchidaceae	58	24	106	72	34	130	0.262	0.185
Apocynaceae	48	13	185	150	35	198	0.177	<i>0.066</i>
Malvaceae	45	14	72	41	31	86	0.360	0.163
Euphorbiaceae	41	17	85	61	24	102	0.235	0.167
Cyperaceae	33	3	58	28	30	61	0.492	<i>0.049</i>
Lamiaceae	31	4	77	50	27	81	0.333	<i>0.049</i>
Sapindaceae	26	12	44	30	14	56	0.250	0.214
Cucurbitaceae	23	9	36	22	14	45	0.311	0.200
Convolvulaceae	21	4	31	14	17	35	0.486	0.114
Amaranthaceae	20	3	67	50	17	70	0.243	<i>0.043</i>
Celastraceae	18	8	37	27	10	45	0.222	0.178
Arecaceae	16	11	23	18	5	34	<i>0.147</i>	0.324
Phyllanthaceae	16	4	25	13	12	29	0.414	0.138
Plantaginaceae	15	5	25	15	10	30	0.333	0.167
Urticaceae	15	1	21	7	14	22	0.636	<i>0.045</i>
Meliaceae	14	7	26	19	7	33	0.212	0.212
Orobanchaceae	13	5	25	17	8	30	0.267	0.167
Apiaceae	13	8	76	71	5	84	<i>0.060</i>	0.095
Melastomataceae	12	3	30	21	9	33	0.273	0.091
Anacardiaceae	11	8	22	19	3	30	<i>0.100</i>	0.267
Primulaceae	11	3	12	4	8	15	0.533	0.200
Gentianaceae	11	3	22	14	8	25	0.320	0.120
Asparagaceae	11	2	42	33	9	44	0.205	<i>0.045</i>
Sarcolaenaceae	10	10	0	0	0	10	<i>0.000</i>	1.000
Moraceae	10	4	15	9	6	19	0.316	0.211
Menispermaceae	10	6	26	22	4	32	<i>0.125</i>	0.188
Salicaceae	10	3	17	10	7	20	0.350	0.150
Commelinaceae	10	3	18	11	7	21	0.333	0.143
Araceae	10	5	32	27	5	37	<i>0.135</i>	0.135
Rhamnaceae	10	1	17	8	9	18	0.500	<i>0.056</i>
Solanaceae	10	1	18	9	9	19	0.474	<i>0.053</i>
Annonaceae	10	2	43	35	8	45	0.178	<i>0.044</i>
Connaraceae	10	0	11	1	10	11	0.909	<i>0.000</i>
...	...	...	...	...	...	...	...	...
Total	1572	471	3996	2895	1101	4467		
Global value							0.246	0.105

family) Primulaceae and Connaraceae (not all shown on table 2).

The global value of similarity between MA and SSA based on the Jaccard index (0.246) is eight times higher than at specific level. High values are found in Connaraceae, Ur-

ticaceae, Primulaceae, Rhamnaceae, Cyperaceae, Convolvulaceae, Solanaceae and Phyllanthaceae. In contrast, low similarity at generic level occurs in Sarcolaenaceae, Apiaceae, Anacardiaceae, Menispermaceae, Araceae, Arecaceae. Among families with lower generic richness in Madagascar

(not shown on table 2), low similarity values are also found in Bignoniaceae, Sapotaceae and Rutaceae.

Madagascar specificity at generic level (see also fig. 4A & B) has a global value of 0.105, which is of course lower than at species level. High values are observed in seventeen of these 38 families, and especially in Sarcolaenaceae, Arecaceae, Anacardiaceae, Acanthaceae, Sapindaceae, Meliaceae, Moraceae and Primulaceae. In contrast, low values (< 0.07) are observed in Connaraceae, Amaranthaceae, Annonaceae, Asparagaceae, Urticaceae, Annonaceae, Asparagaceae, Cyperaceae, Lamiaceae, Solanaceae, Rhamnaceae, Apocynaceae and Asteraceae.

Comparison of the specific richness of genera between Madagascar (MA) and Sub Saharan Africa (SSA)

Table 3 presents specific richness, MA–SAA similarity and MA specificity for the 31 most species-rich genera in Madagascar.

The richest genus in MA is *Bulbophyllum* with 193 species, followed by *Impatiens*, *Dombeya*, *Croton*, *Dyopsis*, *Angraecum* and *Euphorbia*. Eleven genera in the top 31 richest in MA also belong to the top 31 of the whole area. They are (listed by decreasing richness for total area): *Euphorbia*, *Senecio*, *Helichrysum*, *Aloe*, *Vernonia*, *Psychotria*, *Impatiens*, *Cyperus*, *Bulbophyllum*, *Plectranthus* and *Justicia*. Other genera with very high diversity in MA + SSA, but with low richness in MA include typically highly diversified SA genera like *Erica* L., *Thesium* L. and *Pelargonium* L'Hér. ex Aiton (with a few representatives in MA) *Aspalathus* L., *Ruschia* Schwantes or *Lampranthus* N.E.Br. (completely absent from MA). They also include genera whose diversity is mainly in TA like *Crotalaria* L., *Indigofera* L. or *Habenaria* Willd.

Global similarity has of course the same value as presented above (0.029). Twenty-three out of these 31 genera have a much lower value. Among them, a similarity value of zero is found in eleven genera. Three of them have only endemic species in MA (*Dyopsis*, *Pandanus*, *Gravesia*) and one is not represented in SSA: *Anisostachya*. The endemic genera of MA are not represented in this list, the most diverse (*Aspidostemon* Rohwer & H.G.Richt. and *Microsteira* Baker) comprising only 28 species each (Callmander et al. 2011). High values are found in *Kalanchoe*, *Hibiscus*, *Cyperus* and *Panicum* L.

Regarding MA specificity (global value of 0.165, fig. 5), 22 out of the 31 richest genera have significantly higher values and none of them has a low value (< 0.10). Genera for which this MA specificity is maximal include *Bulbophyllum*, *Impatiens*, *Dombeya*, *Dyopsis*, *Croton* and *Angraecum* for the most diverse, but also *Gravesia*, *Cynorkis*, *Oncostemum*, *Hypoestes*, *Memecylon*, *Pandanus*, *Cynanchum*, *Medinilla*, *Secamone* and *Anisostachya*. It is noteworthy that among this list, three genera belong to Orchidaceae.

DISCUSSION

Comparing the angiosperm richness of the three areas

At specific level, MA flora is highly distinct from both TA and SA. In contrast, overlap between TA and SA is high, which is not surprising considering that boundaries between them are political: Southern Africa as circumscribed here contains not only the areas experiencing winter rainfall regime of the Cape Floristic Region (Goldblatt & Manning 2000), but also all the subtropical regions of Southern Africa (notably the Kalahari, the northern provinces of RSA and KwaZulu-Natal) which intergrade with the tropical African flora. Species shared between the three areas are mainly pantropical species (e.g. *Abrus precatorius* L.) or species widely distributed

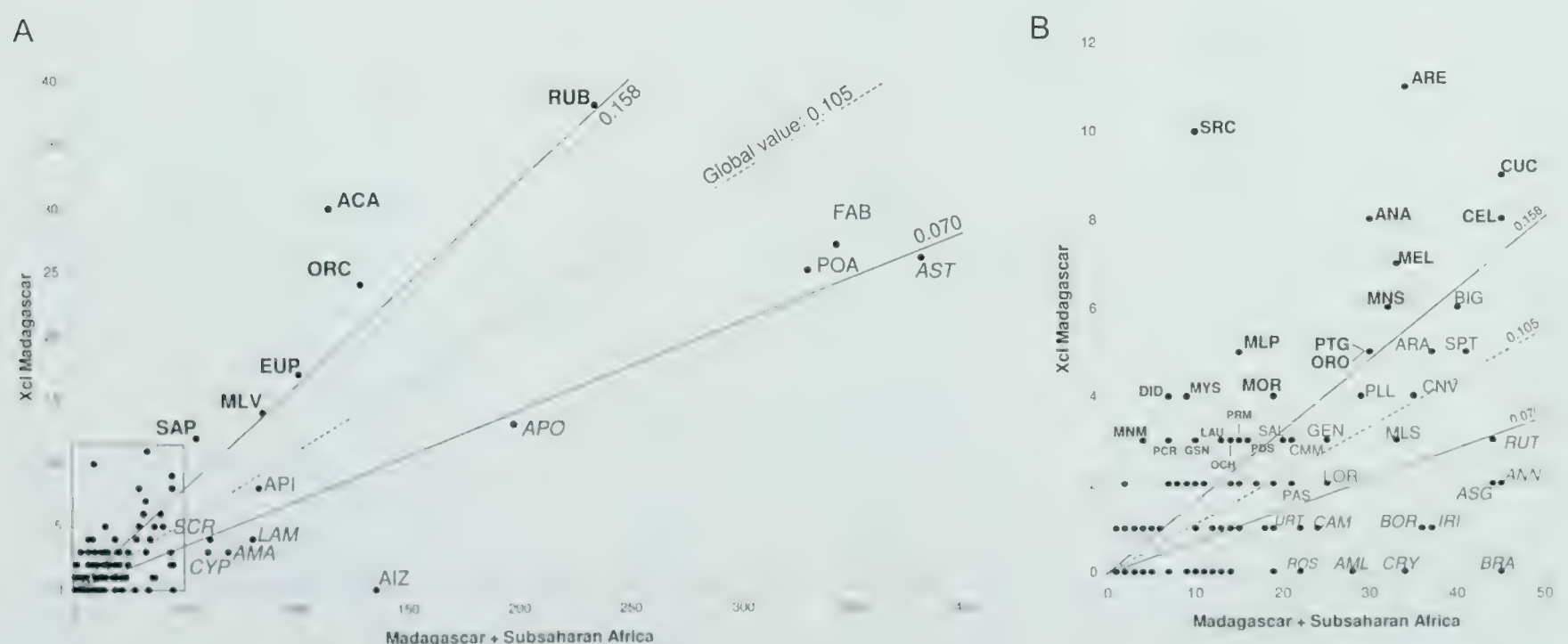


Figure 4 Generic richness of families. X-axis: number of genera in the whole area (Sub Saharan Africa and Madagascar); Y-axis: number of genera occurring only in Madagascar (and possibly elsewhere, but not in SSA). Dotted line: global value for all angiosperms. Solid lines 0.070 ($2/3 \times$ global value) and 0.158 ($1.5 \times$ global value) ratios. Acronyms of families according to Weber (1982). Italics and bold: Families with low (resp. high) Madagascar specificity. A, whole graph; B, detail of bottom-left corner.

Table 3 – Species richness, affinities and Madagascar specificity of the top 31 species-rich genera in Madagascar.
Xcl: exclusively; end: endemics; MA: Madagascar; SAA: Sub Saharan Africa; high values ($> 1.5 \times$ global value) of affinity and specificity in bold, low values ($< 2/3 \times$ global value) in italics.

Genus	Family	Total MA	Xcl MA (end MA)	Total SSA	Xcl SSA	Shared MA / SSA	Total	Similarity	Specificity
<i>Bulbophyllum</i> Thouars	Orchidaceae	193	188 (179)	95	90	5	283	0.018	0.664
<i>Dombeya</i> Lam.	Malvaceae	182	181 (173)	21	20	1	202	0.005	0.896
<i>Impatiens</i> L.	Balsaminaceae	172	171 (171)	125	124	1	296	0.003	0.578
<i>Croton</i> L.	Euphorbiaceae	150	148 (143)	62	60	2	210	0.010	0.705
<i>Dypsis</i> Noronha ex. Mart.	Arecaceae	145	145 (145)	0	0	0	145	0.000	1.000
<i>Angraecum</i> Bory	Orchidaceae	135	133 (120)	54	52	2	187	0.011	0.711
<i>Euphorbia</i> L.	Euphorbiaceae	129	126 (120)	779	776	3	905	0.003	0.139
<i>Helichrysum</i> Mill.	Asteraceae	112	111 (110)	350	349	1	461	0.002	0.241
<i>Gravesia</i> Naudin	Melastomataceae	108	108 (108)	5	5	0	113	0.000	0.956
<i>Psychotria</i> L.	Rubiaceae	103	103 (102)	234	234	0	337	0.000	0.306
<i>Cynorkis</i> Thouars	Orchidaceae	102	102 (91)	18	18	0	120	0.000	0.850
<i>Oncostemum</i> A.Juss.	Primulaceae	100	100 (99)	0	0	0	100	0.000	1.000
<i>Hypoestes</i> Sol. ex R.Br.	Acanthaceae	93	93 (90)	18	18	0	111	0.000	0.838
<i>Aloe</i> L.	Xanthorrhoeaceae	91	90 (90)	320	319	1	410	0.002	0.220
<i>Justicia</i> L.	Acanthaceae	87	83 (83)	161	157	4	244	0.016	0.340
<i>Memecylon</i> L.	Melastomataceae	86	85 (85)	55	54	1	140	0.007	0.607
<i>Diospyros</i> L.	Ebenaceae	86	85 (84)	112	111	1	197	0.005	0.431
<i>Pandanus</i> Parkinson	Pandanaceae	84	84 (84)	60	60	0	144	0.000	0.583
<i>Cyperus</i> L.	Cyperaceae	82	49 (35)	238	205	33	287	0.115	0.171
<i>Cynanchum</i> L.	Apocynaceae	80	77 (77)	35	32	3	112	0.027	0.688
<i>Vernonia</i> Schreb.	Asteraceae	76	71 (70)	310	305	5	381	0.013	0.186
<i>Medinilla</i> Gaudich.	Melastomataceae	70	70 (68)	4	4	0	74	0.000	0.946
<i>Secamone</i> R.Br.	Apocynaceae	70	70 (68)	20	20	0	90	0.000	0.778
<i>Grewia</i> L.	Malvaceae	65	57 (55)	124	116	8	181	0.044	0.315
<i>Kalanchoe</i> Adans.	Crassulaceae	63	50 (48)	72	59	13	122	0.107	0.410
<i>Senecio</i> L.	Asteraceae	63	57 (56)	423	417	6	480	0.013	0.119
<i>Anisostachya</i> Nees	Acanthaceae	60	60 (59)	0	0	0	60	0.000	1.000
<i>Clerodendrum</i> L.	Lamiaceae	60	60 (57)	90	90	0	150	0.000	0.400
<i>Plectranthus</i> L'Hér.	Lamiaceae	53	47 (46)	213	207	6	260	0.023	0.181
<i>Coffea</i> L.	Rubiaceae	52	51 (49)	44	43	1	95	0.011	0.537
<i>Hibiscus</i> L.	Malvaceae	52	35 (32)	173	156	17	208	0.082	0.168
...	...	...	...	...	...	...	...	...	...
Total		10657	9083 (8583)	46016	44442	1574	55099		
Global value								0.029	0.165

in the African region (e.g. *Urera trinervis* (Hochst.) Friis & Immelman or *Ficus lutea* Vahl). Their distribution in Southern Africa is generally limited to the eastern subtropical humid coast of KwaZulu-Natal. With respect to MA however, there are many more species shared with TA than with SA. The number of 49 species shared with SA would probably be reduced to almost zero, if only the overlap with the Cape Floristic Region had been considered.

At generic level, richness ranking of the three areas is the same as for species and the topology of the Venn diagram is similar. However, as expected, the intersections of the Venn diagram are larger. Comparing raw data between specific and generic level is of little interest, the comparison in relative terms is more informative. Taxa that occur in all three areas demonstrate a relative increase of $\times 12$ when the generic level is compared with the specific level. Consequently, number

of taxa restricted to one of the three areas under study is lower: $\times 0.5$ for SA, $\times 0.6$ for MA and $\times 0.7$ for TA. Taxa shared between two areas only have a relative increase of $\times 5.2$ for the TA-MA intersection, of $\times 4.5$ for the SA-MA, but this increase is only of $\times 2.4$ for the TA-SA intersection. Two different characteristics of the floras concerned serve to explain this difference. First the SA flora contains a strong endemic element at the generic level, represented by the numerous endemic genera of the Cape Floristic Region. Second, while the endemism of MA is exceptionally high at specific level, many genera are shared with TA.

Comparing the richness of families and genera between Sub Saharan Africa (SSA) and Madagascar (MA)

Poaceae, Asteraceae, Fabaceae and Rubiaceae are clearly the richest families of the total area under study, both in terms of species and genus richness. Poaceae shows the highest generic and specific similarities between MA and SSA. In contrast, Rubiaceae has a lower similarity between MA and SSA, especially at the specific level, but higher MA specificity, as exemplified by the genus *Psychotria*. The large genera of Fabaceae in Africa are much less well represented in MA (*Crotalaria* and *Indigofera*) or even absent (*Aspalathus*). In Asteraceae however, the large African genera (*Senecio*, *Helichrysum*, *Vernonia*) are generally also well represented in MA.

Orchidaceae is the family with highest specific richness in Madagascar, but ranks only 6th in number of genera. It has a high MA specificity in species, mainly caused by very large genera, three of which are amongst the most diverse in MA

and which each possesses high MA specificity (*Bulbophyllum*, *Angraecum* and *Cynorkis*).

Acanthaceae, Apocynaceae, Euphorbiaceae, Malvaceae and Lamiaceae are next in specific and generic richness in the whole area and in Madagascar. In this group of families, specific similarity is low, except for Malvaceae. Generic similarity is generally above average, with the exception of Euphorbiaceae and Apocynaceae. MA specificity at generic level is high in Acanthaceae, and low in Apocynaceae. In Euphorbiaceae, *Euphorbia* is the largest genus in Africa and is also very diverse in MA, whereas *Croton* has achieved a spectacular richness in MA. Other important genera with high MA specificity in this group of families include *Dombeya* in Malvaceae; *Hypoestes*, *Justicia* and *Anisostachya* in Acanthaceae; *Secamone* and *Cynanchum* in Apocynaceae.

Cyperaceae and Convolvulaceae share a high specific MA/SSA similarity, although Cyperaceae is richer at specific and generic level, while Convolvulaceae displays low MA specificity at species level. The genus *Cyperus* has an average MA specificity, but many species in MA are shared either with SSA or with other areas.

In contrast, some families such as Melastomataceae, Arecaceae, Balsaminaceae, Lauraceae, Primulaceae (incl. Myrsinaceae), Salicaceae (incl. Flacourtiaceae p.p.), Pandanaceae, Ebenaceae, Bignoniaceae and Malpighiaceae are very rich in species in MA compared with SSA; their MA specificity is often in excess of 0.5 which means that they have more species in MA than in the whole of SSA. In general, they display low to very low similarity at specific level and an average to high similarity at generic level (but low in Arecaceae). These families often have several MA endemic gen-

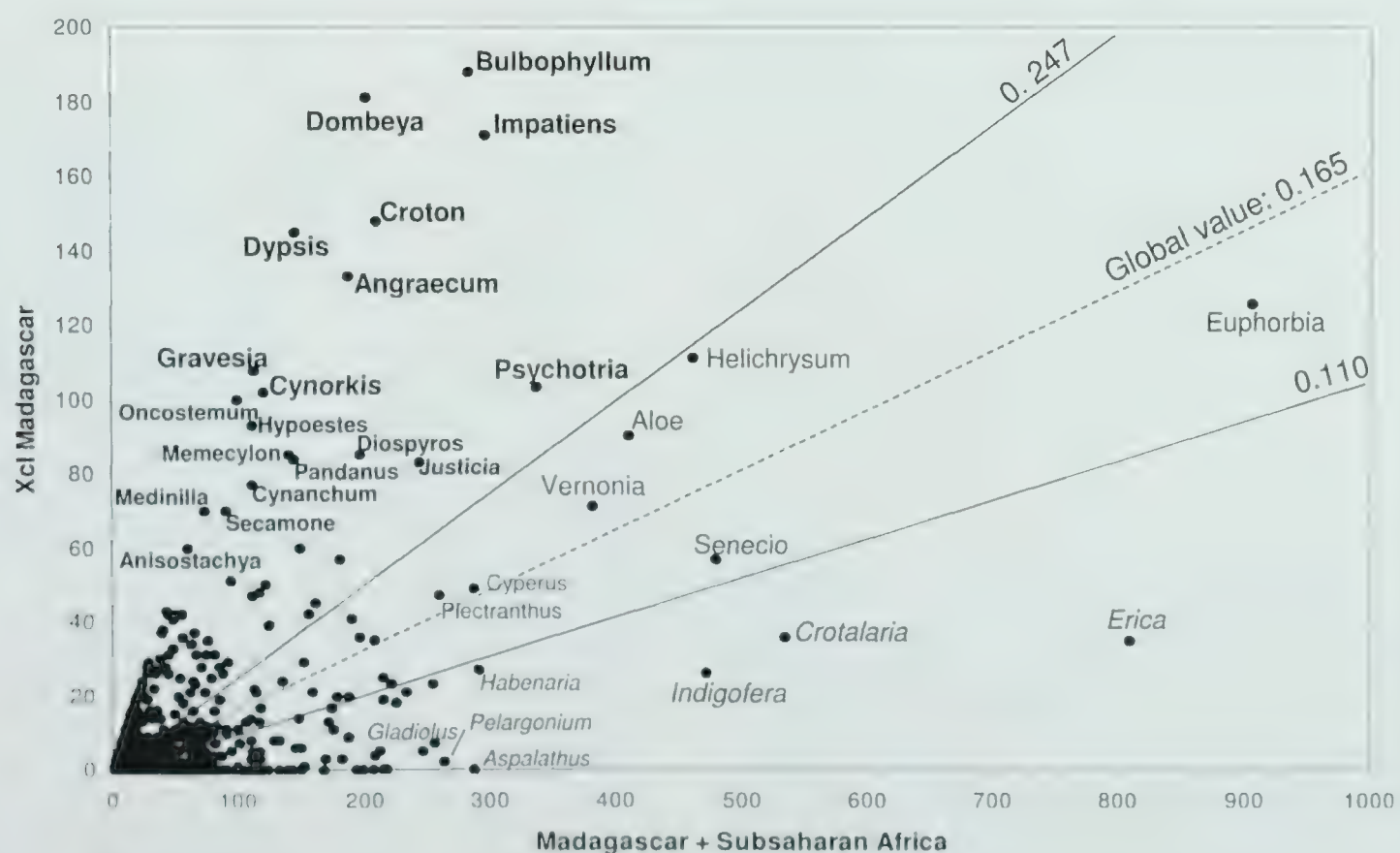


Figure 5 Specific richness of genera. X-axis: number of species in the whole area (Sub Saharan Africa and Madagascar); Y-axis: number of species occurring only in Madagascar (and possibly elsewhere, but not in SSA). Dotted line: global value for all angiosperms. Solid lines 0.110 ($2/3 \times$ global value) and 0.247 ($1.5 \times$ global value) ratios. Italics and bold: Families with low (resp. high) Madagascar specificity.

era (or absent from SSA), some of them being particularly rich: *Oncostemum* in Primulaceae, *Dyopsis* in Arecaceae, and *Gravesia* in Melastomataceae. Their high MA specificity is also the consequence of important non-endemic genera with numerous endemic species like *Memecylon* and *Medinilla* in Melastomataceae, *Ocotea* and *Cryptocarya* in Lauraceae and *Homalium* in Salicaceae. Certain families are exceptions in this group because they consist of a single genus (Balsaminaceae: *Impatiens* and Ebenaceae: *Diospyros*) or almost (Pandanaeae: *Pandanus*).

A further group of families that should be mentioned comprises medium-sized tropical families such as Phyllanthaceae (formerly included in Euphorbiaceae), Sapindaceae, Annonaceae, Celastraceae, Rutaceae, Sapotaceae and Meliaceae. At specific level, these families generally have a low similarity (except Celastraceae) and a relatively rich MA component (except Rutaceae, because of a very high specific richness in SA). At generic level, similarity generally has average values (but high in Phyllanthaceae and low in Rutaceae and Sapotaceae), and relatively high MA specificity (except Rutaceae and Annonaceae).

A set of families with high specific richness in the entire area, but which are species-poor in Madagascar comprises Aizoaceae, Asparagaceae, Iridaceae, Scrophulariaceae, Proteaceae, and Geraniaceae. These families mostly include very large SA genera like *Ruschia* or *Lampranthus* in Aizoaceae, *Gladiolus* in Iridaceae, and *Pelargonium* in Geraniaceae. They consequently have very low similarity values.

The same kind of pattern appears in Xanthorrhoeaceae and Ericaceae, except that these two families are dominated by single genera (*Aloe* and *Erica* respectively) that are also well represented in Madagascar by endemic species.

Among families with less than seventy species in MA, some reach exceptionally high values of MA specificity at specific level (> 0.8). These include MA endemic families (Sarcocaulaceae, Sphaerosepalaceae, Asteropeiaceae, etc.); families that are very poorly represented in SSA like Monimiaceae, Cunoniaceae and Calophyllaceae (formerly included in Clusiaceae), and Elaeocarpaceae. Further families with a very high MA specificity (between 0.5 and 0.8) include Araliaceae, Piperaceae, Erythroxylaceae, Myristicaceae, Talinaceae, Hydrostachyaceae, Didiereaceae and Picrodendraceae.

CONCLUSION

The study confirms the general trends of richness and endemism of the Madagascar flora published so far and provides precise figures based on the current knowledge of taxonomy, representing a valuable up-to-date contribution to the understanding of the relationships between the floras of Africa. Further collaborations will aim at the integration of additional distribution data in the *African Plant Database*, especially for the western Indian Ocean Islands. In addition to the growing body of phylogenetic work, it will contribute to a more in-depth understanding of the fascinating biogeography of Madagascar.

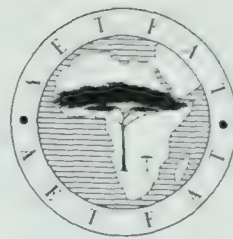
ACKNOWLEDGEMENTS

Authors would like to express their thanks to colleagues at G, PRE and MO that have made this Database a reality and to all botanists in Madagascar and around the world who have contributed to these data through their daily work. Many thanks also to two anonymous reviewers who contributed significantly to the improvement of the manuscript.

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- Manuscript received 31 Oct. 2010; accepted in revised version 1 Dec. 2011. This paper was pre-published on 12 Mar. 2012 in issue 145(1) of *Plant Ecology and Evolution*.
- Communicating Editor: Sylvain Razafimandimbison.



Aloes of the World Project: background and progress

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Background – The Old World genus *Aloe* L. comprises $\pm$ 630 species to which almost 1300 names have been applied. Members of the genus are prominent components of many, mainly arid, African landscapes. Aloes can be found in Africa (the majority of species), the Arabian Peninsula, Socotra, Madagascar and the Mascarene Islands. The berried aloes of the genus *Lomatophyllum* Willd. are included as a section of the genus *Aloe* for the purpose of this project.

Aims – As part of the African Plants Initiative (JSTOR Plant Science), the Aloes of the World project aims to provide a comprehensive electronic facility that pulls together all relevant information and available images in a web-based, user-friendly information base. An electronic interactive key to the genus will also be produced.

Results – The project has shown steady progress over the last five years since AETFAT 2007 in Cameroon. The database currently contains descriptions and additional information for $\pm$ 430 taxa, while several publications have resulted from the project.

Key words – *Aloe*, Asphodelaceae / Aloaceae / Xanthorrhoeaceae, checklist, database, identification key, African Plants Initiative (API), Aloes of the World Project.

INTRODUCTION

The iconic genus of leaf succulents, *Aloe* L. (Asphodelaceae), is represented by approximately 157 endemic taxa on Madagascar and surrounding islands, and a further $\pm$ 470 taxa in sub-Saharan Africa and the Arabian Peninsula. Aloes are of considerable economic importance and have many traditional uses. The natural products from the leaves of some species support local harvesting industries, and many species of *Aloe* are known in horticulture. However, non-sustainable collecting and habitat transformation presents a significant threat to the genus. In recent years, the systematics, taxonomy and conservation of *Aloe* have attracted much research attention and new species continue to be discovered. Considerable advances have been made towards understanding the complex biology of the group, including pollination syn-

dromes, micromorphology, phytochemistry and molecular variation among species of *Aloe*.

The Aloes of the World Symposium, held during the 19th AETFAT Congress in Madagascar in 2010, showcased recent taxonomic and conservation research on the genus *Aloe* in general, in particular the work of contributors to the Aloes of the World project. The AETFAT Congress is a well-established and widely recognised opportunity for local and international scientists working on the floras of Africa and Western Indian Ocean Islands to gather and exchange ideas. With eight oral and three associated poster presentations, this dedicated symposium drew a wide audience at the congress. It proved a valuable occasion to discuss opportunities for the sustainable development of aloes throughout their range, and to establish and refresh collaborations among aloecologists. Current and anticipated outputs of the Aloes of the World

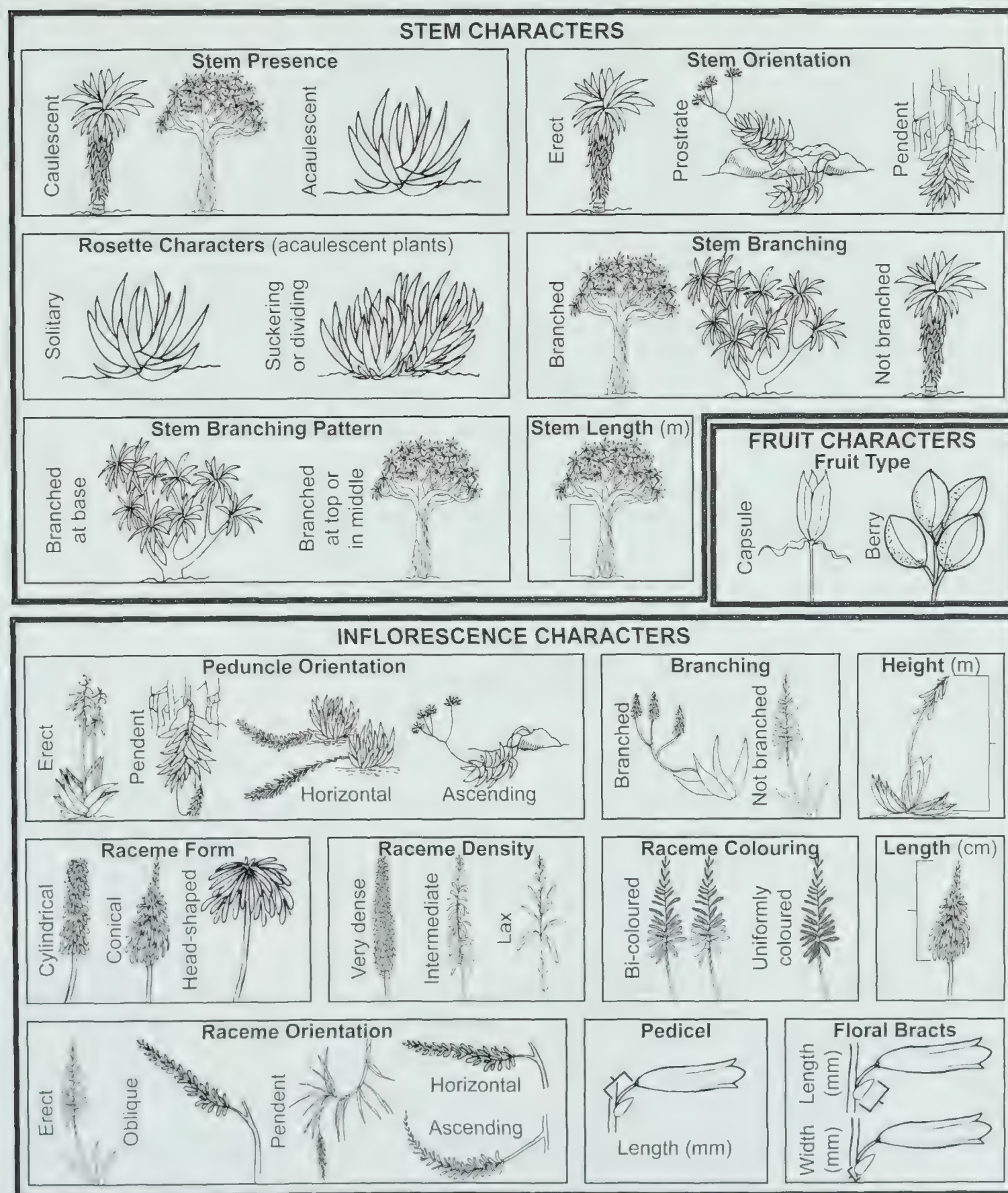


Figure 1 Illustrated Lucid character list: Stem, fruit and inflorescence characters.

project were highlighted to generate support and recognition for this exciting component of the African Plants Initiative (JSTOR Plant Science, formerly 'ALUKA').

BACKGROUND TO THE ALOES OF THE WORLD PROJECT

The Aloes of the World Project aims to provide a comprehensive electronic facility that pulls together all relevant information and available images in a web-based, user-friendly information base. This is being achieved through an international collaborative effort that includes all interested aloe experts from around the globe. The project is funded by the

Andrew W. Mellon Foundation through the African Plants Initiative (API).

Although there is a wealth of information available on the genus *Aloe*, the information is widely disbursed and inevitably not easily accessible to the global community of *Aloe* enthusiasts and interested gardeners. The Aloes of the World project aims to ensure that diverse information about representatives of the genus is available online. A further aim is to build capacity and skill a new generation of *Aloe* specialists, through information, and knowledge transfer. The project hopes to generate interest among young scientists and thus create a vibrant scientific *Aloe* research community that is sustained well into the future.

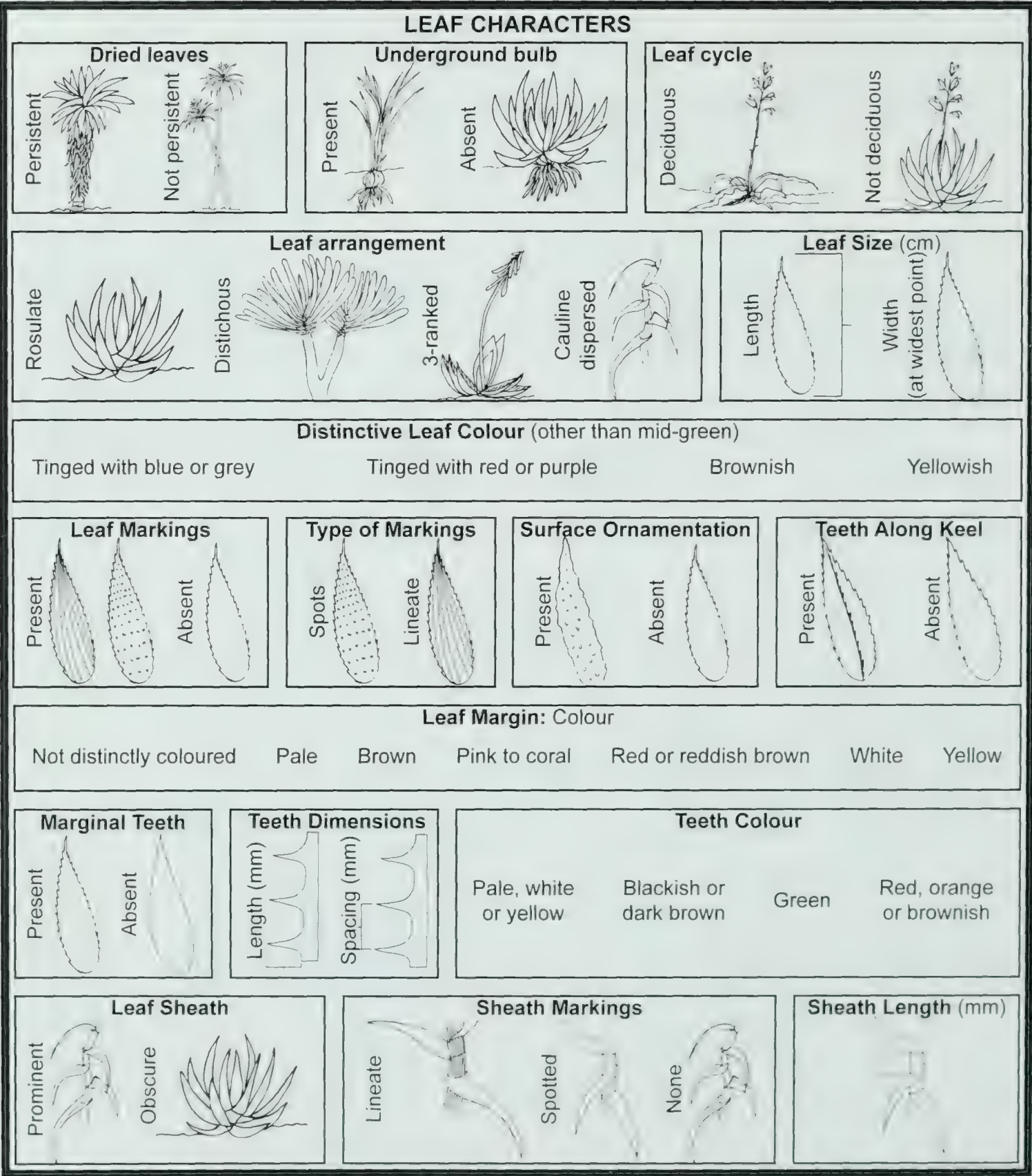


Figure 2 – Illustrated Lucid character list: Leaf characters.

The main outputs of the project are the compilation of information and images into a web-based, user-friendly information base. The accessibility through the internet of this comprehensive electronic facility will be facilitated by JSTOR through the API project, and will be available at <http://plants.jstor.org> at the end of the project. Further outputs are:

- 1) A checklist to the genus and also regional or country checklists.
- 2) Regional treatments of aloes. These usually contain identification keys, descriptions for the taxa, distinguishing characters, distribution maps, images, and additional information such as flowering time, habitat, common names, etc.

- 3) Probably the foremost output is an electronic interactive identification key to the entire genus, using Lucid software. This will be published on the internet (most likely at <http://www.lucidcentral.com>) and could also be made available on CD or DVD.

ALOES OF THE WORLD WORKSHOP.
19–22 NOVEMBER 2007

The project was initiated in 2007, when a workshop was conducted in Pretoria with ± 40 experts attending from all over the globe; a prerequisite for success has been broad international support for the project. One of the main aims of the workshop was to determine scholarly needs in relation to ongoing research on aloes, and how this could be serviced

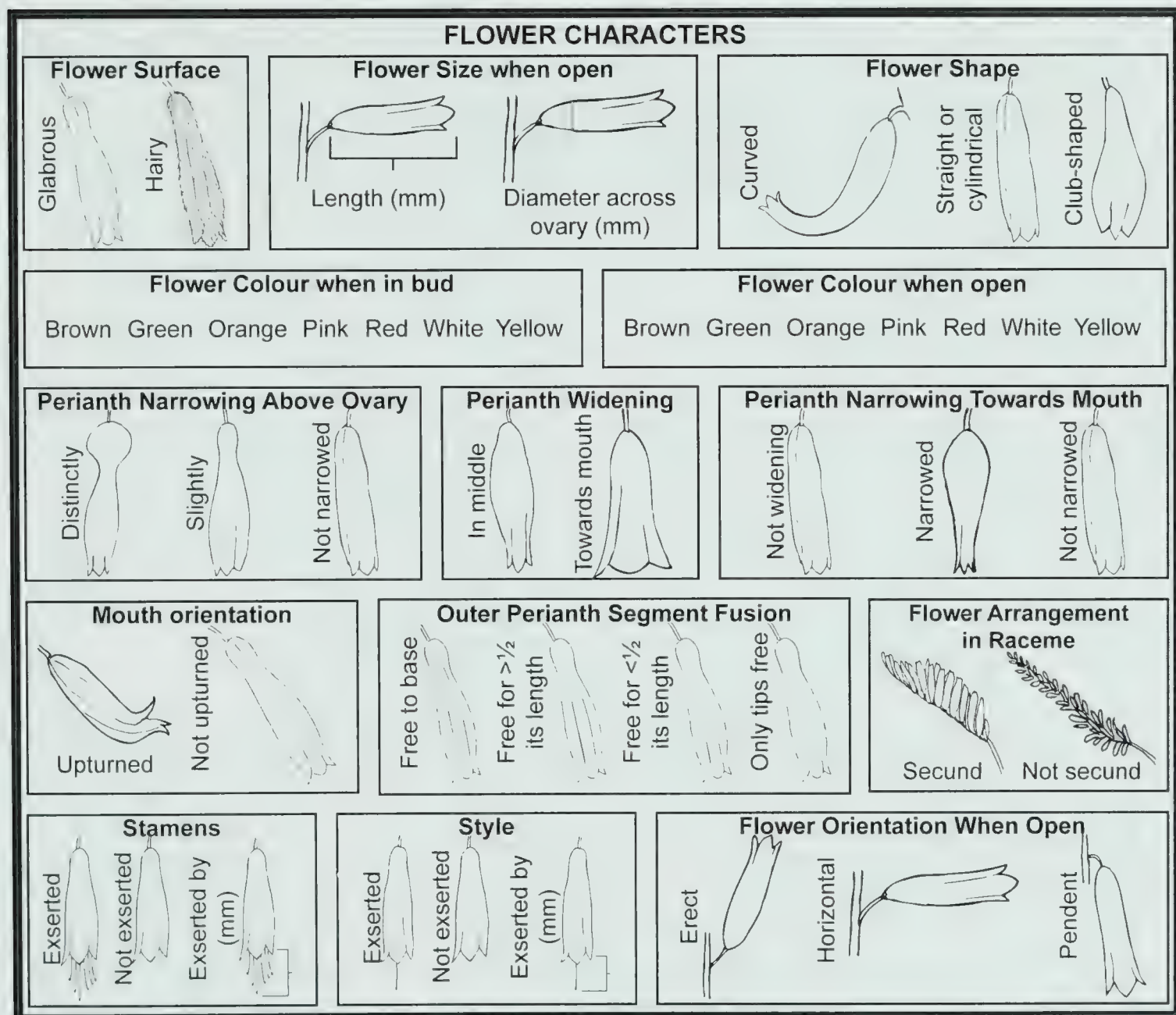


Figure 3 – Illustrated Lucid character list: Flower characters.

through an internet-based facility. This workshop was the first event of its kind to deal exclusively with *Aloe*.

During this workshop several issues around the project was discussed. Major outputs from the workshop included:

- 1) Agreement on *Aloe* content the group wanted to have hosted by JSTOR.
- 2) Abbreviated and comprehensive description templates to be used in the descriptions of taxa.
- 3) Lucid character list to be used in the interactive key.
- 4) The workshop report (Smith et al. 2008a, 2008b).

Through a positive atmosphere the workshop succeeded in creating an information-generating network consisting of young experts as well as established scientists.

PROGRESS

General

Names, descriptions and additional information are held in an MS Access database, from where checklists, regional treatments and other combinations of the available information can be extracted with ease. The Aloes of the World database currently holds:

- A total of 1292 plant names of which 626 are current.

- Descriptions for 436 taxa, or roughly 70% of the genus.
- A total of 1199 literature references, including many protologues.
- Etymologies describing the origin and history of some 880 aloe epithets (Figueiredo & Smith 2010).
- A total of 1519 common names of aloes in 164 languages from around the world (Grace et al. 2011).
- Chromosome numbers of 137 taxa.
- Phenologies for 345 taxa.
- Habitat notes for 563 taxa.
- A total of 989 entries dealing with type specimens and associated data, e.g. collector and number, date when collected, locality, herbarium where deposited, barcode number, etc.

Checklists

Checklists for the following areas or countries are complete:

- The Succulent Karoo biome
- Namaqualand
- The Fynbos biome
- The Western Cape, Eastern Cape, Northern Cape, Free State and KwaZulu-Natal provinces of South Africa
- Angola (Klopper et al. 2010)
- Malawi

- Zimbabwe
- Ethiopia (Sebsebe Demissew & Nordal 2010; Sebsebe Demissew et al. 2011)
- Madagascar and the Western Indian Ocean Islands (Klopper et al. 2013).

Regional treatments

- Regional treatments for the following areas are complete and most have already been published:
- The Succulent Karoo biome (Klopper & Smith 2008)
- Namaqualand (Klopper & Smith 2007)
- The Western Cape, Eastern Cape (Klopper & Smith 2010), Northern Cape and Free State (Klopper et al. 2009b) provinces of South Africa
- Angola (Klopper et al. 2009a)
- Malawi (Klopper et al. 2012)

Maps

Maps for around 138 taxa have been finalised, with several others in the process of completion. This is an area where the project will soon focus more intensely. For the southern African taxa, production of maps is not that problematic. However, for many other regions the absence of, or unavailability of informative maps and gazetteers are complicating the process. It is here where the help of project collaborators, resident in or well-acquainted with the areas and/or taxa concerned, will prove to be of the utmost importance.

Interactive identification key

The Lucid character list and glossary has been illustrated (figs 1–3). Coding of taxa in the interactive key is in progress. The 27 Angolan taxa were used as a pilot project to test the key. During this initial testing phase the key has proved very useful in readily identifying these taxa, using a minimum of characters.

Future prospects

The Aloes of the World project has succeeded in enabling growth of a network of experts, and in shaping a mutually beneficial, truly international, and effective collaboration that collates and shares information about the genus. This collaboration will hopefully continue well into the future, beyond the official project funding phase.

SUPPLEMENTARY DATA

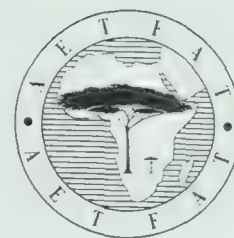
Supplementary data are available in pdf at the Supplementary Data Site of publications from the National Botanic Garden of Belgium (<http://www.nbgpublisher.be> > SBB50 > folder 550): electronic appendix containing the three figures (illustrated Lucid character list) in colour plate.

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Manuscript received 1 Oct. 2010; accepted in revised version 23 May 2011.

Communicating Editor: Sylvain Razafimandimbison.



The Global Plants Initiative (GPI) and the California Academy of Sciences

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Background – In 2004, the Andrew W. Mellon Foundation began funding a digital database of botanical type specimen images and label data for the African Plants Initiative (API) followed by the Latin American Plants Initiative (LAPI) in 2007. These projects have evolved into today's Global Plants Initiative (GPI). The GPI was originally designed to electronically repatriate images of type specimens collected from continental Africa, Madagascar, and surrounding islands; by its third year, the Initiative boasted nearly fifty partner institutions.

Current Status – Today, the project has developed a global focus currently supporting approximately 195 partner institutions. In addition to high-resolution type specimen images, the database amasses collection information, photographs, botanical illustrations, taxonomic and other relevant literature, and related data. To date, more than 900,000 images are available on the JSTOR Plant Science website (<http://plants.jstor.org>). In Madagascar, both Parc Botanique et Zoologique de Tsimbazaza (TAN) and Centre National de la Recherche Appliquée au Développement Rural (TEF) were early participants in the project. They have jointly submitted 1260 type specimen images to this project.

CAS Participation – The California Academy of Sciences began active participation in 2008 with our Latin American and African type specimen images; we continue to image type specimens from our worldwide collection. As of early 2011, we have submitted more than 10,000 images.

Benefits – Immediate benefits of the GPI initiative include electronic access to type specimen images by more than one researcher simultaneously without the need to travel to repository institutions and a significant reduction in type specimen loans with a corresponding reduction in potential loss or damage during shipment.

Key words – African Plants Initiative (API), digital database, Global Plants Initiative (GPI), JSTOR, type images, JSTOR Plant Science.

INTRODUCTION

The Global Plants Initiative (GPI) is a worldwide project funded by the Andrew W. Mellon Foundation. GPI developed from an earlier Mellon-funded project that originated as the result of discussions held during the 2003 meeting of the Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale (Association for the Taxonomic Study of the Flora of Tropical Africa, AETFAT). The following is a brief review of GPI and a discussion of the participation of the California Academy of Sciences (CAS; San Francisco, California, USA) in this project.

Because of the history of exploration, many early botanical type specimens were removed from their countries of origin and housed in herbaria in Europe and the United States of America. This made the specimens difficult to access for

researchers in those countries of origin. In 2004, the Andrew W. Mellon Foundation began funding a digital database of botanical type specimen images and label data for the African Plants Initiative (API). The program was expanded to include other bibliographic and archival materials used by researchers. In 2007 this initiative was further expanded to include vascular plant type specimens from Latin American countries: the Latin American Plants Initiative (LAPI). Both API and LAPI were designed to electronically repatriate images of botanical type specimens and make them available to a global audience.

This current, worldwide project is now referred to as the Global Plants Initiative (GPI). Data is organized and stored on a JSTOR website (<http://plants.jstor.org>). JSTOR, an acronym for "journal storage" is an online archiving system originally funded by the Andrew W. Mellon Foundation. As

a specialized interface of JSTOR, it is hoped that GPI will become self-supporting in future years, although the exact nature of this self-support is still under discussion. In the project's third year, there were approximately 50 partner institutions. By 2011, the project with its global focus involved approximately 195 partner institutions (electronic appendix 1).

CAS PARTICIPATION IN GPI

The herbarium at CAS houses approximately 2 million plant specimens including approximately 12,000 vascular plant type specimens. Nearly 40% of these type specimens are from Latin American countries; because of this, CAS was contacted and invited to participate in the LAPI project. At that time, we were in temporary quarters preparing to move into a new building on our former site in San Francisco's Golden Gate Park. By the time we were able to begin participation, the API/LAPI project had expanded to include all vascular type specimens worldwide. This expansion allowed us to include all of our type specimens, including those from Africa and Madagascar. The Academy has an active research and training center in Madagascar, the Bibikely Biodiversity Center. Researchers using this and other logistical facilities in Antananarivo have recently deposited several type specimens of Malagasy vascular plants at Parc Botanique et Zoologique de Tsimbazaza (TAN), CAS, and other institutions with an interest in the flora of Madagascar.

All GPI partners follow a common protocol when scanning images. This ensures that the images can be compared accurately online. Scans are made using the HerbScan™, a device developed by Andrew McRobb, photographer at the Royal Botanic Gardens, Kew (fig. 1). The HerbScan supports the type specimen face-up on a foam-covered support; a pulley system gently raises the specimen to an inverted scanner (modified to operate 'upside-down' and with the lid removed), and a scan is made at 600 dots-per-inch (dpi) resolution (fig. 2). The resulting images are approximately 200 MB in size. Each image includes a barcode specific to the home institution, a standardized color chart, and a short metric ruler (fig. 3). Each scan is produced with identical Photoshop color settings and with no Photoshop adjustments (e.g. sharpening, screening). When the image is viewed online, a magnified version can be observed with an online measuring tool that can be calibrated to the scanned ruler, ensuring accurate measurements to tenths, even hundredths, of millimeters. Small details involving shape, texture, and trichome form and density are easily viewed on the screen (fig. 4).

Fragment packet contents are scanned and 'pasted' onto the image so that researchers can see exactly what detached materials are available for study on each specimen. Some type specimens that have been scanned at CAS lacked fragment packets; others had packets containing enough material to fill a second sheet. Some specimens have multiple packets, each of which must be opened so that the contents can be scanned. Some CAS types are simply fragments, probably small pieces from another institution's type specimen. One of the smallest such type specimens at CAS was collected by Charles Darwin in the Galapagos Islands.

All partners are required to perform a quality check on the images and related data generated at their home institu-

tions. Colleagues at Kew developed a method of reviewing images using a free software application called 'IrfanScan'; the method easily reveals inadvertent scanning problems. The primary quality problem encountered at CAS was related to individuals leaning on the HerbScan while it was in use. Other problems have been caused by dust on or within the scanner.

Data from the specimen label and annotations are entered in a database. Some CAS specimens have a great deal of information on the label; others have very little. Each partner institution may select its own method of capturing data. CAS



Figure 1 HerbScan™ in closed (scanning) position; for information on obtaining the HerbScan device, please contact herbscan@mac.com



Figure 2 – HerbScan™ with specimen in open position.

currently uses an open source software program called Specify for its herbarium database. We strive to capture as much data as possible; however, we submit only required information (such as basionym, collector, country of origin) to the GPI site.

When we have accumulated approximately one thousand images, the related data is converted into xml (eXtensible Mark-up Language) format. We have developed an internal quality check for content; this was necessary because our database contains an amalgam of information imported from several individually created databases using various software applications (e.g., dBase III, Access, Excel). Sometimes, information was imported incompletely or incorrectly. Our most common xml data problem has been with missing author information. As part of our quality check, we also ensure that xml data conforms to GPI standards and check it with an online xml syntax tool. Finally, we ascertain that each image has corresponding xml data.

Each batch of data and images is submitted to JSTOR where it undergoes another quality check. After images and data are posted online, GPI participants can continue to correct or update information using an online tool called 'Xumba'. Using Xumba, participants can view their types, upload new images, and make corrections to the xml data through this password-protected interface.

Participation in the Global Plants Initiative has provided a welcome opportunity to review, verify and update the da-



Figure 3 – Scan of type specimen of *Pseudocalyx macrophyllus* McPherson & A. Lewis.

tabase for our vascular plant type specimens. At CAS, the type specimens are filed alphabetically by basionym without regard to family and stored separately from the general collection. Some of our type specimens show little or no annotation history; others are heavily annotated.

BENEFITS OF GPI

There are several advantages to having type images available on a searchable web site. GPI electronically repatriates specimens and ancillary materials, making them available to researchers in their countries of origin as well as researchers with a particular taxonomic or geographic focus. Because high-resolution images are available online, the images are available to more than one researcher simultaneously without the need to travel to repository institutions. Type specimens will no longer be sequestered in an institution for an extended period while on loan to a researcher for a special study. Researchers can now see which participating herbaria house which type specimens for virtually all taxonomic groups without on-site visits. It is also anticipated that there will be a significant reduction in type specimen loans with a corresponding reduction in potential loss or damage during shipment.

The JSTOR Plant Science website is useful not only to view type images. Many species, particularly African plant

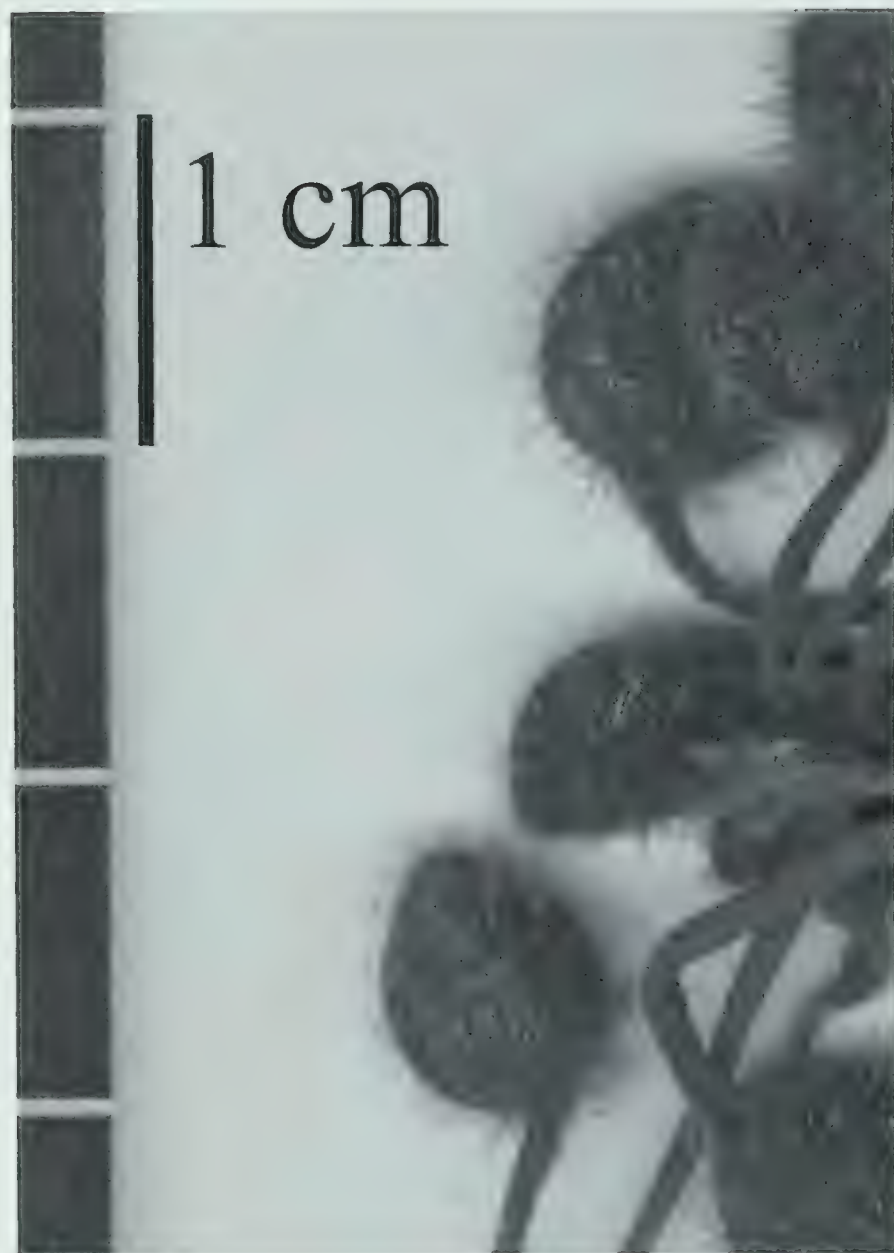


Figure 4 – Detail of scan made at 600 dpi.

species, are also depicted in habit photos and/or included in checklists and floras. For a given species, a researcher may be able to view the holotype and several isotypes. At the time of the 19th AETFAT Congress, nearly 800,000 images were available online on the GPI JSTOR site. At the time of this writing (September, 2010), a list of the more than one million materials now online includes artifacts, books and articles; diaries, letters, notes, and manuscripts; drawings, sketches, prints, illustrations, and engravings; slides and photographs; and more than 900,000 type specimens. In Madagascar, both TAN and Centre National de la Recherche Appliquée au Développement Rural (TEF) were early participants in the project. They jointly submitted 1,260 type specimen images to this project. At the time of the 19th AETFAT Congress, CAS had submitted 5600 images; and at the time of this writing, we had sent more than 9,700 images. By the end of 2011, we hope to have completed imaging our flat type specimens.

ISSUES AND SOLUTIONS

We are certain that online accessibility will enhance the use and ease the burden of acquiring critical specimens for research and other projects. This online accessibility also provides an easy way for specialists to quickly correct, verify, or update information on electronic images of type specimens at any partner institution. We can now receive notifications of readily correctable problems with a simple e-mail communication. Many common problems, such as misspellings or missing information, can be corrected online via Xumba. Partners are developing protocols to electronically annotate specimens.

Some type specimens are too bulky to scan: either the process would damage the specimen or the specimen is too thick to fit under the scanner. Partners at Kew have developed a camera set-up that is portable so that one camera can capture images for several institutions. The high resolution of this camera allows the creation of images that are comparable in quality to the scanned images of flat specimens.

When the 19th AETFAT Congress convened in April, 2010, the Foundation was still accepting new partners. Institutions with few type specimens could participate as collaborators with larger partner institutions (examples of this form of collaboration are listed in electronic appendix 1). The Foundation began funding matching requests for the camera setup to image bulky specimens in 2010.

SUPPLEMENTARY MATERIAL

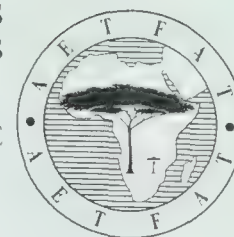
Supplementary data are available in pdf at the Supplementary Data Site of publications from the National Botanic Garden of Belgium (<http://www.nbgpublisher.be> > SBB50 - folder 533) and consist of a list of partner Institutions and collaborators of Global Plants Initiative.

ACKNOWLEDGEMENTS

The authors would like to thank the Andrew W. Mellon Foundation for support and assistance and for their vision to help create this extraordinary scholarly resource; our colleagues at partner institutions who have helped with our participation; our Malagasy colleagues who presented this paper when we were unable to attend the Congress because of disrupted air service brought on by the Iceland volcano ash cloud; our colleagues at the California Academy of Sciences, and our reviewers who made many useful suggestions.

Manuscript received 29 Sep. 2010; accepted in revised version 29 Jun. 2011.

Communicating Editor: Thomas Janssen



Utilisation et conservation durable des ignames du corridor forestier Ambositra-Vondrozo, Madagascar

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Sustainable use and conservation of yams in Ambositra-Vondrozo forest corridor, Madagascar

Context – This pilot project focuses on yam conservation in Ambositra-Vondrozo forest corridor (COFAV) through population studies of wild species and the adoption of new methods of cultivation of the introduced species *Dioscorea alata* L.

Methods – The research was done in collaboration with local community associations. The project aimed to determine levels of exploitation of yams and their importance compared with other foods. Twenty village associations (Vondron’Olona Ifotony or VOI) were selected and enquiries were made in 700 households following training. Plots were established to track the population size of yams through the seasons. The project also helped selected communities and households to cultivate the ‘ovibe’ (*Dioscorea alata* L.), an economically viable alternative to travelling long distances to exploit wild forest yams.

Key results – Wild yam species have become rare in COFAV due to forest fragmentation and unsustainable collecting of yam tubers for food. Moreover, knowledge of both cultivated and wild yams in this region is incomplete and currently there is no management plan to conserve yams in their natural habitat. Forty-three herbarium specimens of yams (*Dioscorea* spp) were collected during inventory work. In parallel, 800 plants of ‘ovibe’ (*Dioscorea alata*) were cultivated by these VOIs, producing a total of 1 ton of tubers at the end of the growing season. Most VOIs decided to continue ‘ovibe’ cultivation at the end of the project. Their objective was to ensure sufficient food production to protect the wild yams and their sites from over-use.

Conclusion – The modern cultivation technique for ‘ovibe’ (*D. alata*) adopted by the villagers was identified as the priority action for this project. Once this method of culture was established locally, visits to the forest decreased in frequency. This should allow the wild species to regenerate in their natural environment.

Key words – Villagers association, conservation, corridor, *Dioscorea*, Madagascar, ovibe, sustainable use, yam.

Contexte – Ce projet-pilote portait sur la conservation et la protection des ignames dans le corridor forestier d’Ambositra Vondrozo (COFAV), à travers l’étude des populations d’espèces sauvages et l’adoption de nouvelles méthodes de culture de l’espèce introduite *Dioscorea alata* (L.), ou ‘ovibe’.

Méthodes – Le projet a été réalisé en collaboration avec les associations représentant les communautés locales. Le but était de déterminer les niveaux d’exploitation des ignames et leur importance par rapport aux autres aliments. Vingt associations villageoises (Vondron’Olona Ifotony ou VOI), ont été sélectionnées et, après formation, ont enquêté auprès de 700 ménages. Des plots ont été mis en place pour étudier les populations d’ignames sauvages. Le projet a aussi encouragé les ménages à cultiver l’‘ovibe’ (*Dioscorea alata* L.), ce qui représente une alternative économique viable à l’exploitation des ignames sauvages, exigeant de longs trajets pour leur récolte.

Résultats-clés – Les espèces d’ignames sauvages du COFAV se sont raréfiées à cause de la déforestation, et de la récolte intensive de leurs tubercules. En outre, la connaissance sur les ignames de cette région est insuffisante, et aucune stratégie de gestion durable de ces ressources n’est encore mise en oeuvre. Les

membres des VOIs ont collecté 43 échantillons d'herbier d'ignames (*Dioscorea* spp.) après inventaire, et planté 800 pieds d'ovibe' (*Dioscorea alata* L.), leur permettant de récolter à la fin de la saison de culture près d'une tonne de tubercules. A la fin du projet, la plupart des VOIs ont décidé de continuer la culture d'ovibe'. L'objectif poursuivi était d'assurer une production alimentaire suffisante pour protéger les populations d'ignames sauvages d'une surexploitation.

Conclusion – La technique moderne de culture de l'ovibe' (*D. alata*) fut identifiée comme l'action prioritaire de ce projet. Lorsque cette méthode de culture est adoptée localement, on constate un déclin de la récolte d'ignames sauvages dans le milieu forestier. Ceci devrait permettre aux espèces sauvages de se régénérer dans leur environnement naturel.

INTRODUCTION

Le corridor forestier d'Ambositra-Vondrozo (COFAV) est une forêt humide linéaire au Sud Est de Madagascar. Depuis 2005, ce corridor fait partie des nouvelles aires protégées créées dans l'ex-province de Fianarantsoa, avec une superficie d'environ 499 600 ha (Ganomanana 2011). Il renferme notamment une flore endémique à la région. Par exemple, Wilkin et al. (2008) ont mentionné l'existence de trois espèces d'ignames endémiques aux forêts humides de Madagascar: *Dioscorea kimiae* Wilkin, *Dioscorea madecassa* H.Perrier et *Dioscorea seriflora* Jum. & H.Perrier. Comme les autres ignames Malagasy, ces espèces occupent divers types d'habitats dans le COFAV, aussi bien sur des terrains cultivés que dans des forêts primaires plus ou moins dégradées (Jeannoda et al. 2007). A cause des différentes pressions anthropiques, les ignames du COFAV sont menacées d'extinction. En effet, la déforestation continue à modifier leur habitat naturel. La superficie de la forêt de basse altitude du COFAV a presque disparu à cause de l'occupation des bas-fonds du corridor par la population locale à croissance démographique galopante (Ganomanana 2011).

Face à ce problème, le Royal Botanic Gardens Kew en collaboration avec Feedback Madagascar – Ny Tanintsika, le Département de Biologie et Ecologie Végétales de l'Université d'Antananarivo, et le projet Crop Wild Relatives ont initié un projet pilote dont l'objectif consiste à maintenir la richesse spécifique des ignames Malagasy tout en encourageant une exploitation durable et une technique de culture adaptée à la population locale. Afin d'atteindre cet objectif, l'approche communautaire a été adoptée pour la mise en œuvre de toutes les activités planifiées. Après formation de certains groupes cibles, les communautés locales du COFAV ont considéré la nouvelle technique de culture d'ovibe' (*Dioscorea alata* L.) comme une des solutions efficaces pour lutter contre la déforestation et la malnutrition.

Les résultats de ce projet permettraient de vulgariser la multiplication d'ignames à proximité des villages ruraux afin d'assurer une meilleure conservation des ignames sauvages. De telles informations sont utiles aux décideurs environnementaux pour la mise en cohérence des actions de conservation avec celles du développement.

METHODOLOGIE

Les ignames sauvages de la partie orientale de Madagascar présentent une large diversité spécifique (Wilkin et al. 2008).

De nombreuses données et informations importantes sur ces espèces, leur habitat ainsi que leur environnement restent toutefois à découvrir.

Pour cette étude, notre approche s'appuie sur trois étapes successives. Tout d'abord, des méthodes d'enquêtes auprès de la population locale ont été effectuées afin de sélectionner les sites d'études et de choisir les communautés de base participantes dans le projet. Ensuite, des méthodes de plots ont été utilisées pour inventorier les espèces d'ignames sauvages dans le corridor forestier d'Ambositra-Vondrozo. Et enfin, l'utilisation de la technique moderne de culture d'ignames a été adoptée par les communautés villageoises.

Les communautés ont participé dans la mise en œuvre de ces activités, et ils ont reçu des séries de formations sur les différentes méthodes de travail adoptées.

Méthode d'échantillonnage des sites d'intervention et des communautés participantes

La méthode d'échantillonnage consiste à sélectionner quelques sites et les communautés de base pour la mise en œuvre des activités du projet. C'est une méthode courante utilisée pour une étude ethnobotanique, écologique et socio-économique en milieu rural. Des enquêtes ont été effectuées auprès des villageois du COFAV en considérant certains critères: les sites plus accessibles et plus proches de la forêt primaire, l'enthousiasme et la motivation des communautés de base à participer dans le projet. Pour l'inventaire des ignames sauvages, des parcelles ont été délimitées à l'intérieur des divers types de formations végétales accessibles; le nombre d'espèces et le nombre d'individus ont été recensés et ont fait l'objet d'une étude écologique.

Méthode de collecte des données socio-économiques

Lors du lancement du projet avec le promoteur, des informations générales sur les ignames ont été recueillies sur certains sites. Des questionnaires simples basés sur ces informations préalables ont été ensuite élaborés dans le but de mieux connaître la situation socio-économique de la population riveraine du corridor forestier. Les questionnaires d'enquête varient suivant les ménages et les villages ciblés, mais sont tout de même complémentaires.

L'appendice électronique 1 donne en détail les types de questionnaire établis. Les questionnaires de type A et B sont focalisés sur l'utilisation et l'importance économique des ignames dans chaque foyer visité. Par contre, les questionnaires du type C tiennent compte de l'avis public sur l'igname et sa conservation dans la forêt du COFAV. Dans ce

cas, l'enquête était plus ouverte et les neuf questions établies dans cette catégorie sont complémentaires et préparées pour certains groupes-cibles ou 'focus groups'. Pour ces groupes-cibles, l'enquête a été effectuée sous forme de réunions durant lesquelles les hommes et les femmes ont fait l'objet d'enquêtes séparées.

Pour une réunion, il faut d'abord faire une demande auprès du chef fokotany, qui est le chef de plusieurs villages regroupés. Ensuite, il faut arranger avec lui le bon moment pour rencontrer le public. Par ailleurs, il faut aviser plusieurs jours les personnes cibles avant la rencontre. Pour ce, toute convocation a été publiquement affichée au bureau du fokotany en précisant les catégories du public à enquêter.

Méthode de collecte d'herbiers et des informations écologiques des ignames sauvages

Cinq plots ont été tracés et délimités à l'intérieur des différents types de végétation; les espèces d'ignames sauvages trouvées y ont été inventoriées et quelques spécimens d'herbiers de ces dernières y ont été collectés. Suivant la disponibilité des plantes, l'inventaire a été effectué autour des villages et dans les forêts et les VOIs ont choisi eux-mêmes leurs sites d'intervention. En une journée de collecte par semaine pendant le mois d'octobre en 2008, 43 échantillons d'herbiers ont été récoltés au total et ils ont été déposés dans un endroit sec et bien aéré pour leur conservation.

Pour étudier les caractères écologiques des ignames inventoriées, le nombre d'individus de chaque espèce a été compté et leur phénologie a été observée. Leurs types d'habitat, et leur localisation par rapport aux villages ont été aussi notés par les VOIs participants. Une base de données simple a été créée pour enregistrer toutes ces informations obtenues sur terrain.

Méthode de culture d'ignames

Quelques ignames cultivées existent déjà et associées avec d'autres plantes dans des champs de culture des villageois de la région du COFAV. Ces pratiques n'utilisent cependant aucune technique particulière. Pour améliorer la production d'ignames comme source alimentaire pendant la période de soudure, le projet a offert aux membres des communautés locales une formation sur la méthode de 'minisets'. Il s'agit d'une technique d'obtention de plusieurs semences à partir d'un tubercule coupé en petits morceaux de même taille. C'est la technique de culture utilisée à Madagascar et vulgarisée par le Programme SAHA depuis plusieurs années. En une saison de culture d'igname, les VOIs formés ont pratiqué cette méthode quelque soit les particularités écologiques des plots de démonstration.

RESULTATS

Les sites d'intervention du projet et les associations villageoises (VOI)

Le tableau 1 présente les quatorze VOIs et les seize fokotany répartis dans les deux principaux districts de la région du COFAV, Ikongo et Ambalavao, sélectionnés comme sites d'intervention prioritaires. Ce sont des sites localisés aux

alentours du corridor forestier (appendice électronique 2) situés à une distance comprise entre 500 m et 10 km à vol d'oiseau de la forêt primaire. Quatorze associations villageoises ou VOIs ont été choisies pour participer dans le projet puisqu'elles représentent la population locale et possèdent seulement le droit de contrôler l'accès aux ressources naturelles.

Résultats des enquêtes des ménages – Plus de 700 ménages ont été visités et enquêtés par les VOIs (appendice électronique 3). La plupart se trouvent sur les bas-fonds du corridor forestier, considérés comme les zones les plus arables de la région. Les ménages enquêtés sont tous des cultivateurs; ils s'intéressent principalement à la riziculture, mais aussi à d'autres cultures de plantes à tubercules comme les patates douces et les maniocs, et à la culture de légumes et d'arbres fruitiers. En outre, la culture de café est pratiquée sur les sites depuis une vingtaine d'années. La production est moindre et n'arrive pas à satisfaire les besoins de la population locale. La culture de vanille et de canne à sucre constitue une source de revenu importante pour les habitants de la région du COFAV. La plupart des ménages pratiquent d'une part la culture sur brûlis pour l'extension de leur culture et d'autre part le feu de brousse pour l'élevage extensif de zébus dans les prairies.

La pratique répétitive du feu d'Août à Octobre a comme conséquence la perte de la forêt et l'appauvrissement du sol (Kull 2004). Ce cas se présente actuellement dans la forêt du COFAV qui diminue en largeur, de 50 km à l'heure actuelle si seulement 15 km il y a quelques années (Mohamed 2008). En fait, les villageois de cette région abandonnent les anciens plots et brûlent systématiquement les nouvelles parcelles rencontrées pour une culture de deux à trois ans, et ainsi de suite. Le sol devient alors de plus en plus pauvre, mais l'insuffisance du rendement agricole reste toujours un des problèmes socio-économiques les plus graves pour les habitants. Pendant les quatre mois de période de soudure où il y a rupture du stock de riz, le problème de nourriture s'amplifie et seuls les tubercules d'ignames sont disponibles à consommer. Chaque ménage possède au moins un champ de culture d'ignames, mais seulement avec quelques pieds par plot. Il a été constaté que les villageois s'intéressent surtout à la culture de l'espèce *Dioscorea alata* L. (appendice électronique 4A) communément appelée 'ovibe' parce qu'elle peut produire d'énormes tubercules, la récolte pouvant atteindre des dizaines de kilos par pied.

Différentes sortes de *Dioscorea alata* existent dans la région du COFAV. Le nom vernaculaire change suivant leur caractéristique. On appelle 'ovy ramiendaka' les tubercules de couleur rouge après épluchage, donnant l'image d'une jambe blessée. Parfois, on utilise le terme 'ovy tranga' quand les tubercules se développent vers la surface; il est facile de les discerner au ras du sol. Un autre terme intervient également lorsque les tubercules s'enfoncent très profondément dans le sol et présentent parfois des traces comparées aux briques de mur superposées. Dans ce cas, on donne le nom 'ovy rindrina' qui se traduit littéralement 'mur d'igname'.

L'existence d'une autre espèce d'ignames cultivées dans la région du COFAV a été confirmée pendant les enquêtes. Il s'agit du 'hofika' ou *Dioscorea bulbifera* L. qui est une

Tableau 1 Les villages et les fokotany des district d’Ikongo et d’Ambalavao concernés dans le projet.
Informations détaillées obtenues auprès des VOIs. *: un fokotany est constitué de plusieurs villages.

Nom des VOIs	Fokotany*	Village	Commune rurale	Date de création du VOI	Nombre des membres du VOI	Surface de la forêt gérée	Distance de la forêt par rapport aux villages
Zanasakana	Ambohimahasoa	Anaviavy	Maromandra	2005	40	Vohitramdriambavy & Ambohimita	4000–9000 m
Fiarenana	Mandriandry, Madiorano, Ambodivavana	Kianjamiakatra, Ambodivavana	Tolongoina	12 Jan. 2000	VOI Fiarenana: 30, VOI Madiorano: 80	Amboasary, 5 ha 227 a	3000–10000 m
Ranomby	Tsaratanana	Tsaratanana	Ambatofotsy	10 Nov. 2002	160 hommes et 20 femmes	5800 ha	100–6000 (1000–20000) m
Marolala	Antaranjaha	Tsararano	Ambolomadinika	2003	40	10 ha	100–4000 m
Alampo	Marolita	Marolita	Ambatofotsy	10 Nov. 2002	220	1700 ha	500–1500 m
Sambatra	Antarehimamy	Antarehimamy	Ambolomadinika	2003	63	15 ha	3000–5000 m
Isitraka	Ankatsaoka	Ankatsaoka	Ikongo	10 Nov. 2003	45	50 ha	500–3000 m
Miray	Ambohimahavelo	Ambohimahavelo	Ikongo	10 Nov. 2003	45	600 ha	1000–4000 m
Zafindrahakaha	Ambatombitro	Ambatombitro	Ankarimbelo	22 Déc. 2005	137	990 ha	1000–5000 m
Analamamitra	Ambalagoavy	Ambalagoavy	Ikongo	2003	160	470 ha	3000–8000 m
Inyady	Ambalahosy	Ambalahosy	Ankarimbelo	Déc. 2005	56	465 ha	8000–35000 m
ETFE MA Vohiboay	Vohiboay	Vohiboay	Miarinarivo	29 Sep. 2001	360	1800 ha	500–3000 m
Lovavasa	Andohammanamandana	Ankarinombo Nord	Ambohimahamasina	2003	30	500 ha	3000–6000 m
Itaolana Mijoro	Itaolana	Itaolana	Ambohimahamasina	2003	200	500 ha sur une surface totale de 2839 ha	1500–3500 m

plante invasive avec des bulbilles et des tubercules toxiques. Suivant leur forme, le degré de toxicité des tubercules varie. Les plus arrondis sont les plus toxiques (appendice électronique 4B), et sont plutôt utilisés pour traiter certaines maladies bénignes comme les furoncles et les brûlures. Les ‘hofika’ à tubercule plus anguleux (appendice électronique 4C) sont toutefois comestibles après traitements (Burkill & Perrier de la Bâthie 1950). Ces procédés ont surtout lieu en cas de disette. Les populations locales mangent le ‘hofika’ cuit après avoir submergé les tubercules dans de l’eau courante pendant une semaine pour les débarrasser de leur toxine. Selon les ménages enquêtés, le mode de cuisson du ‘hofika’ est la même que celui d’‘ovibe’ une fois la toxine extraite. Ils peuvent être préparés en ‘sambaika’, un repas salé, ou en ‘kadaka’, un peu sucré, selon la préférence. Les villageois ont aussi mentionné que la plupart des tubercules d’ignames débarrassés de leurs toxines restent frais et peuvent être consommés au plus tard quatre jours après leur récolte. En outre, il s’avère nécessaire pour les villageois d’envisager la vente des tubercules aux marchés locaux en cas d’excès de production. Cependant, la vente locale d’ignames sur les marchés du COFAV est rare pour deux principales raisons: tout d’abord, il existe peu d’acheteurs car presque tous les paysans en cultivent; ensuite, les villageois ne sont pas motivés à vendre en raison du poids des tubercules d’ignames, souvent lourd et donc difficiles à transporter, le marché se trouvant souvent très éloigné des champs de culture. De plus, le coût de l’igname est seulement d’environ 800 Ariary le kilo, ce qui ne couvre donc pas leur frais de déplacement.

D’après les habitants du COFAV, la quantité d’ignames disponibles dans la région du COFAV reste insuffisante surtout pendant la période de soudure. Pour eux, l’igname ne constitue pas une source de revenue adéquate pour les ménages jusqu’à présent.

Résultats des enquêtes des groupes-cibles (focus groups)

Des enquêtes sous forme de réunions ont été organisées dans les 21 fokotany (appendice électronique 3) en rassemblant les villageois, les autorités locales et les membres des VOIs responsables de chaque site concerné.

A chaque réunion, l’assistance a toujours mentionné que les ignames sauvages deviennent de plus en plus rares dans la forêt du COFAV. Elle a compris que la déforestation détruit les sites des ignames sauvages et qu’il faut désormais aller de plus en plus loin des villages pour en trouver. Une marche d’une demi-journée est nécessaire pour arriver aux sites de collecte des tubercules d’‘ovitarettra’ ou ‘ovilava’ (*Dioscorea kimiae* Wilkin, appendice électronique 4D), et l’‘ovy mariky’ (*Dioscorea arcuatinervis* Hochr., appendice électronique 4E), les deux espèces les plus prisées par les habitants. Malgré leurs tubercules très fins et difficiles à déterrer, les paysans ont récolté ces ignames depuis des générations puisqu’elles sont plus savoureuses par rapport aux autres espèces, sauvages ou cultivées. La récolte de ces deux espèces dans la forêt se pratique surtout en période de soudure. D’après les ménages interrogés, les villageois repèrent l’emplacement des pieds d’ignames dans la forêt un an avant le déterrage pour faciliter leur cueillette la saison suivante.

La technique de cueillette des tubercules d’ignames sauvages par les villageois détruit le sol et empêche la régénéra-

Tableau 2 – Les espèces d’ignames inventoriées par les membres des VOIs.

Espèces identifiées pendant et après la récolte des herbiers.

Noms d’espèces	Nombre d’échantillons
<i>Dioscorea arcuatinervis</i> Hochr.	2
<i>Dioscorea seriflora</i> Jum. & H.Perrier	15
<i>Dioscorea alata</i> L.	17
<i>Dioscorea sansibarensis</i> Pax	3
<i>Dioscorea esculenta</i> (Lour.) Burkill	1
<i>Dioscorea</i> sp.	3
<i>Trichopus sempervirens</i> (H.Perrier) Caddick & Wilkin	2
Total	43

tion de la plante. Les villageois laissent ouverts les trous de déterrage et ne remettent pas en terre la tête des tubercules afin qu’elle puisse se régénérer. En conséquence, les ignames sauvages du COFAV sont donc menacées d’extinction en raison de la technique de récolte utilisée par les villageois.

Résultat des inventaires des espèces d’ignames – D’après le tableau 2, l’espèce *Dioscorea alata* a été la plus représentée dans la collecte des ignames effectuées par les VOIs pendant l’inventaire. Ceci peut être expliqué par le fait que les récolteurs n’ont pas eu vraiment le courage d’aller chercher très loin les ignames qui étaient à ce moment là en phase de dormance (Jeannoda et al. 2007). Quatre autres espèces sauvages ont été répertoriées dans la liste, et la plupart des échantillons représentatifs étaient stériles.

Une autre espèce très ressemblante aux ignames a été également inventoriée. Il s’agit du *Trichopus sempervirens* (H.Perrier) Caddick & Wilkin, appartenant également à la famille des Dioscoreaceae, mais qui est une plante hermaphrodite (Caddick et al. 2002).

Résultat de l’étude écologique des populations sauvages d’ignames – Sur les cinq plots tracés, quatre ont été riches en ‘ovy taretra’ ou *Dioscorea kimiae* Wilkin (tableau 3). C’est une espèce de la forêt orientale de Madagascar d’après Burkill & Perrier de la Bâthie (1950). Elle n’a pas été trouvée par les membres des VOIs pendant la collecte d’échantillons d’herbier à cause de sa localité restreinte et loin des villages. De nombreux jeunes individus d’‘ovy taretra’ ont été trouvés (tableau 3) et présentent une bonne régénération dans des sites plus ou moins ouverts. Par contre, peu d’individus de ‘mariky’ (*Dioscorea arcuatinervis*) ont été recensés à l’intérieur des plots. Cette espèce exige des conditions écologiques particulières, c’est pourquoi elle est plus rare que *Dioscorea kimiae* dans la région du COFAV. Du point de vue morphologique, les tubercules de *Dioscorea arcuatinervis* présentent des ramifications, le permettant de produire de grosses quantités de tubercules par rapport à *Dioscorea kimiae*.

Essai de culture d’‘ovibe’ (*Dioscorea alata*)

Depuis quelques années, le Programme SAHA a vulgarisé la technique de culture par ‘minisetts’ de *Dioscorea alata*

Tableau 3 – Les cinq plots de suivi des populations d’ignames sauvages.
Informations obtenues lors des travaux de terrain. M, pieds matures; J, pieds jeunes.

Nom scientifique	Nom vernaculaire	District d’Ikongo			District d’Ambalavao	
		Sahafy	Andranomay	Lavahatoka	Bevandrika	Analavory
<i>Dioscorea kimiae</i> Wilkin	ovy taretra	13 M	23 M	18 M	21 M	9 M
		65 J	146 J	49 J	305 J	64 J
<i>Dioscorea arcuatinervis</i> Hochr.	Mariky	-	-	24 M	-	-
				171 J		

Tableau 4 – Résultat de la culture d’‘ovibe’ (*Dioscorea alata*).
Information obtenue sur le terrain pendant les visites des cinq plots choisis.

District	Ikongo	Ikongo	Ambalavao	Ambalavao	Ambalavao	Total
Village/commune participants	Tolongoina	Marohita	Sendrisoa	Miarinarivo- Antsahamatilo	Miarinarivo- Ambalaiava	
Surface des plots de démonstration (ares)	9.50	21	200.5	150.5	100.5	482
Type du substrat de chaque plot	latéritique	sablonneux	baiboho	rocailleux	sablonneux	
Tubercules distribuées aux VOI pour semences (kg)	125	125	125	125	125	625
Tubercules obtenus à la fin de la première saison de culture (kg)	122,23	17,2	594,9	290,16	111,55	1136,04
Différence (kg)	- 2,77	- 107,8	469,9	165,16	- 13,45	511,04
Rendement (kg/are)	- 0,29	- 5,14	2,34	1,10	- 0,13	1,06

à Madagascar. Pour la région du COFAV, certains VOIs ont déjà essayé de planter l’‘ovibe’ suivant cette méthode de culture et ils ont déjà des notions sur la valeur nutritionnelle de cette espèce cultivée (appendice électronique 5). Ainsi, RBG Kew et ses partenaires ont offert aux VOIs une nouvelle opportunité de cultiver des ignames pour obtenir de nouvelles semences et une source de nourriture, surtout pendant la période de pénurie de riz. Après la formation des VOIs sur la méthode de plantation d’ignames, la culture d’‘ovibe’ a été réalisée dans cinq plots de démonstration proposés par les associations villageoises elles-mêmes (tableau 4). Selon les indications et instructions fournies aux VOIs au cours des formations théoriques, les terrains riches en matières organiques comme les ‘bahiboho’ sont les meilleurs pour la culture d’‘ovibe’. Pourtant, il faut que ce type de terrain ne soit pas trop près d’une rivière pour éviter la pourriture des tubercules lors de leur croissance sur les champs. Suivant le type de terrain disponible, le choix de l’emplacement des plots choisis par les VOIs n’est pas tout à fait identique.

Seuls les VOIs localisés à Sendrisoa du district d’Ambalavao ont trouvé une parcelle de ‘baiboho’. C’est un terrain plat à quelques centaines de mètres d’une rivière avec un substrat brun sombre riche en matières organiques. Pour les deux autres VOIs sis à Marohita Ikongo et à Miarinarivo Ambalavo, ils ont trouvé des terrains plats mais à substrat sablonneux. A Marohita, le plot tracé se localise trop près d’une rivière et il a été par conséquent totalement inondé pendant la saison de pluie juste avant le temps de déterrage des tubercules d’igname. Par contre le terrain à Miarinarivo a été bien entretenu puisqu’il est entouré par d’autres champs de culture presque visités tous les matins par les VOIs responsables. D’autre part sur le site de Miarinarivo, un deu-

xième plot a été délimité mais sur une pente rocailleuse plus ou moins raide. Ce choix a été fait afin de comparer le résultat obtenu avec celui qui se trouve sur le sable. Dans le village de Tolongoina Ikongo, le plot de démonstration est plus ou moins sec avec un substrat latéritique de couleur rouge.

Au moment de la récolte au bout d’une année de culture, les cinq VOIs ont obtenu au total environ une tonne de tubercules (tableau 4). Puisque le type de terrain de culture et la taille des parcelles choisies n’étaient pas les mêmes, le rendement varie d’un site à un autre. Le VOI à Sendrisoa a été le plus productif avec de près de 600 kg de tubercules, cinq fois plus que le poids de la semence fournie. Ceci peut être expliqué par le fait que ce VOI a bien respecté la technique de culture d’‘ovibe’. Il a compris que les tubercules d’ignames se développent énormément dans un sol meuble et pour que la production soit suffisante, il faut un champ de culture de grande taille.

Par contre à Marohita, 17 kg seulement de tubercules ont été obtenus par le VOI. C’est la production la plus médiocre des VOIs participants à cause de l’emplacement du plot mal choisi, sa taille insuffisante et son entretien mal organisé. On peut constater ainsi que le VOI de Marohita n’a pas bien suivi les importantes consignes fournies lors de la formation.

Sur le sol ferrallitique de Tolongoina et les pentes rocailleuses de Miarinarivo à Ambalavao, la production a été moindre, puisque le poids des tubercules obtenus (122,23 kg) a été presque le même que celui des semences fournies (125 kg). Dans ces deux cas, le substrat est dur et il ne favorise pas du tout le développement des tubercules. Par ailleurs, la surface du plot installé par le VOI de Tolongoina n’a pas été suffisante et le problème d’érosion s’est produit sur la pente forte du plot du VOI à Miarinarivo.

Tous ces résultats conduisent à conclure qu'une production élevée de tubercules d'ignames nécessite donc un sol riche et facile à travailler. En outre, il faut bien respecter la taille et la distance de chaque pied pour la plantation pour que chaque tubercule gagne de la place suffisante à son développement. La taille du champ de culture détermine également la quantité de tubercules obtenus.

A la fin de la récolte, certains tubercules ont été stockés pour servir de semences pour la prochaine saison de culture. A la fin du projet, une visite d'échange et de partage d'idées sur la plantation de cette espèce d'igname a été organisée à Miandrivazo avec les autres VOIs venant d'Ankarafantsika – Mahajanaga. Durant sept jours de rencontre, les VOIs d'Ikongo et d'Ambalavao ont présenté le résultat de leur culture suivi par des discussions avec les autres participants. Une rencontre avec Ravolondolo, un cultivateur local d'ovibe à Miandrivazo, a été également réalisée lors de cette visite. Cet homme possède un champ d'ovibe d'environ deux hectares sur lequel il obtient plusieurs tonnes de tubercules pour chaque période de récolte. Devant cette situation, il a évoqué la nécessité de fournir de meilleures techniques de transformation des tubercules d'ignames pour les conserver plus longtemps. Ce voyage a intéressé les VOIs et les a motivé d'avoir leurs propres champs de culture d'ignames et d'en produire une quantité suffisante pour subvenir aux besoins alimentaires des habitants du COFAV.

DISCUSSION ET RECOMMANDATIONS

La conservation des ignames sauvages du COFAV en collaboration avec les communautés de base fait partie de l'objectif principal du projet pilote. Les principales activités programmées au début du projet ont généralement été réalisées. Pour progresser et améliorer les méthodes d'approche et de travail avec les villageois, quelques recommandations sont toutefois présentées ci-dessous.

Enquête des villageois

Le taux d'alphabétisation et de scolarisation sont très faibles dans la région du COFAV. La plupart des ménages sont pauvres et n'ont pas les moyens d'envoyer leurs enfants à l'école. De plus, l'école publique se trouve souvent à plusieurs heures de marche des villages. De ce fait, il a été assez difficile pour les membres des VOIs de bien compléter les questionnaires et les fiches d'enquête qui leur ont été confiés. Il a été découvert pendant les enquêtes que les habitants du COFAV commencent à vraiment s'intéresser aux ventes locales des tubercules d'ignames, transformés ou non. Pourtant, ils ont peur d'avoir un excès de production et de ne pas trouver de moyens de stockage et de conservation sûrs pour les tubercules d'ignames. En conséquence, les techniques de stockage et de transformation des tubercules, suivies par l'apprentissage de bonnes méthodes de vente constituent d'importants thèmes à considérer ultérieurement dans le projet. La réalisation de ces futurs objectifs va conduire à une sauvegarde des ignames sauvages par la diminution de leur cueillette massive et agressive dans la forêt et une amélioration de la sécurisation alimentaire de la population locale.

Inventaire des ignames

La formation sur l'étude écologique des ignames sauvages a été organisée d'une façon plus claire et simple pour être facilement assimilée par les VOIs participants. A la fin de la formation, les VOIs ont pu d'une part distinguer les ignames des autres plantes qui lui ressemblent, et d'autre part énumérer les caractères morphologiques de chaque échantillon d'herbier qu'ils ont monté. L'absence des organes reproducteurs a rendu complexe l'identification de certaines espèces. Il est donc préférable de programmer les récoltes aux stades de floraison de chaque espèce, pendant la saison pluvieuse, pour bien distinguer les pieds mâles des pieds femelles. En cas d'absence des appareils végétatifs et reproducteurs, certaines espèces peuvent être identifiées à partir de la forme et la couleur de leurs tubercules. Pour ce, il faut bien repérer la période favorable au déterrage des individus, pour ne pas gaspiller les plantes disponibles dans le milieu naturel. Pour l'analyse d'ADN, il s'avère nécessaire de collecter les feuilles seulement pendant la saison de pluie où les feuilles sont abondantes et ne se fanent qu'au bout de six mois.

Etude écologique des populations d'ignames sauvages

Cinq plots de suivi ont été installés à l'intérieur des forêts et d'autres formations secondaires pour l'étude de population des ignames sauvages. Ils sont facilement accessibles et presque à proximité des villages. Afin d'assurer un résultat fiable de ce suivi écologique, il est indispensable d'établir un accord de collaboration avec les VOIs partenaires.

Culture d'ovibe (*Dioscorea alata*)

A propos de la culture d'ovibe, les habitants du COFAV s'intéressent beaucoup à la nouvelle méthode appliquée sur les plots de démonstration des VOIs. Pourtant, il leur faut un apprentissage, à commencer par la pratique sur leur propre parcelle. Par ailleurs, les VOIs formés ont partagé leur connaissance de cette méthode aux autres villageois à la fin du projet. Actuellement, douze nouvelles associations sont prêtes à adopter cette technique de culture dans le but d'améliorer la multiplication de tubercules d'ignames dans la région du COFAV. En cas d'un surplus de tubercules, des séances de transformation des tubercules, suivant différentes méthodes, ont été planifiées pour le futur. Ce qui peut encourager les ménages à continuer leur effort sur la production massive d'ignames leur permettant de fournir une source de revenu supplémentaire. La domestication des ignames sauvages sera prochainement tentée dans différents sites en collaboration avec ces ménages expérimentés.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible au format pdf sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> > SBB50 > dossier 530) et comprend: (1) questionnaires utilisés dans l'enquête auprès des membres des fokotany; (2) carte des sites d'étude du projet; (3) pour chaque fokotany, nombre de ménages concernés par le projet; (4) espèces d'ignames présentes dans le COFAV; et (5) analyse des

valeurs nutritionnelles des ignames malagasy par rapport à d'autres plantes vivrières.

REMERCIEMENTS

Ce projet a pu être réalisé grâce à la participation des partenaires du Royal Botanic Gardens, Kew. Nous remercions également le Ministère des Eaux et Forêts, le Madagascar National Parks et le Parc Botanique et Zoologique de Tsimbazaza qui nous ont accueillis chaleureusement à chaque visite; le Département de Biologie et d'Ecologie Végétales de l'Université d'Antananarivo qui nous a partagé ses expériences sur les ignames; les Techniciens du Feedback Madagascar – Ny Tantintsika qui ont étroitement collaboré avec les VOIs sur le terrain; le Projet Crop Wild Relatives (CWR/FOFIFA), qui nous a aidé financièrement pour la mise en œuvre des activités du projet; tous les personnels du RBG Kew pour leurs conseils techniques et leur collaboration en particulier Dr Rakotoarinivo Mijoro, et les associations villageois ou VOIs et d'autres responsables locaux dans les districts d'Ikongo et Ambalavao qui ont travaillé ensemble pour la réussite du projet.

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Manuscript received 24 Sep. 2010; accepted in revised version 24 Feb. 2012.

Communicating Editor: Rainer Bussmann.



Accroissement en diamètre de trois espèces de palissandre (*Dalbergia chlorocarpa*, *D. lemurica*, *D. purpurascens*, Fabaceae) dans la forêt dense sèche de Kirindy, Morondava (Madagascar)

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Diameter growth of three palisander species (*Dalbergia chlorocarpa*, *D. lemurica*, *D. purpurascens*, Fabaceae) in the dry forest of Kirindy, Morondava (Madagascar)

Background and aims – *Dalbergia* species, referred to as palisander, provide precious woods highly appreciated for cabinet making in Madagascar. They are intensely and selectively logged. Sustainable management and long term timber production based on functional system, in particular the growth, is to be formulated. The aim is to study the growth and the parameters which influence it in order to define the optional rotation period for resource management.

Methods – Yearly measurements of tree growth of three *Dalbergia* species from two different sampling plots were undertaken. The annual diameter increment was calculated. Limiting factors of growth such as local competition between trees for resources, were calculated. Effects of the various factors, logging, station conditions, and competition for growth were analyzed.

Key results – The results revealed that the tree annual diameter increment is lower than 2 mm. The diameter increment is not significantly different between the three species, between the plots and under the competition phenomena. Based on growth data obtained, *Dalbergia* trees with more than 5 cm dbh takes approximately 213 years to produce a tree with 37 cm diameter at breast height (maximal dbh observed in the two plots) in Kirindy forest.

Conclusion – The diameter increment study of three *Dalbergia* species permits to define the recovery of exploitable stock and optional rotation period for sustainable resources.

Key words – *Dalbergia*, growth, diameter, competition indices, logging, dry forest, Kirindy, Madagascar.

Contexte et objectifs – Les espèces de *Dalbergia*, plus connues sous le nom de palissandre, sont des bois précieux très prisés sur le marché de bois d'œuvre à Madagascar. Elles font l'objet d'une exploitation sélective de plus en plus intense. Des mesures de gestion durable basées sur les connaissances du fonctionnement des espèces de *Dalbergia* dont la croissance, doivent être formulées. L'objectif est d'étudier la croissance et les facteurs pouvant l'influer en vue de déterminer le temps de reconstitution des stocks exploitables et de la périodicité des prélèvements dans le cadre de l'aménagement.

Méthodes – Des mesures annuelles de diamètre des individus ont été effectuées durant trois années dans deux parcelles différentes. L'accroissement courant annuel de diamètre a été calculé. Les facteurs influençant la croissance, relatifs à la compétition pour les ressources, ont été calculés. Les effets des différents facteurs, exploitation, conditions stationnelles, compétitions sur la croissance ont été analysés.

Résultats – Les résultats montrent des valeurs d'un accroissement annuel en diamètre inférieurs à 2 mm. La croissance ne diffère significativement pas entre les espèces, entre les parcelles et n'est pas influencée par des phénomènes de compétition. Il faudrait environ 213 ans pour qu'un pied de *Dalbergia* de 5 cm de diamètre atteigne 37 cm de diamètre à hauteur de poitrine (DHP maximal mesuré dans les deux parcelles) dans les conditions environnementales de Kirindy.

Conclusion – L'étude de la croissance des trois espèces de *Dalbergia* permet d'estimer la reconstitution des stocks et la durée de rotation des prélèvements.

INTRODUCTION

Les espèces de genre pantropical *Dalbergia*, connues à Madagascar sous le nom commercial de palissandre, sont des bois d'œuvre classés parmi les bois précieux utilisés pour l'ébénisterie et la menuiserie fine. Par ses bonnes qualités technologiques, bois dur, lourd (Gueneau & Gueneau 1969), les consommateurs nationaux ont une préférence sans équivoque pour cette essence (Andriambanona 2001). Le palissandre est très demandé sur le marché national des bois d'œuvre qu'il domine largement. Sur le marché international, les exportations de palissandre pratiquées depuis l'époque de la colonisation constituent une rentrée de devises pour le pays. Depuis des années, les espèces de *Dalbergia* font l'objet de prélèvements sélectifs non planifiés et de plus en plus intenses dans tout le pays pour assurer les demandes sans cesse croissantes sur le marché. Ce mode d'exploitation accroît leur raréfaction et constitue une grave menace pour la survie du palissandre. En effet, le prélèvement des individus semenciers, sans assurer le potentiel de régénération, diminue la chance de multiplication de ces espèces et peut même entraîner leur disparition. Les espèces de *Dalbergia* pourront également subir une érosion génétique à cause de la raréfaction des semenciers de bonne qualité. D'ailleurs, une vingtaine d'espèces de *Dalbergia* sur les 48 identifiées et publiées à Madagascar sont classées en danger par l'IUCN depuis 1994 (IUCN 2001). Les trois espèces qui font l'objet de cette étude sont classées vulnérables.

L'alternative aux pratiques d'exploitation actuelles est d'assurer la production durable de palissandre sur le marché de bois d'œuvre. Or il est nécessaire, à cet effet, de s'appuyer sur des connaissances détaillées de la survie des espèces de *Dalbergia*, de leur croissance et de leurs caractéristiques de reproduction en forêt naturelle. Cette étude de la croissance qui est l'un des paramètres de la dynamique forestière constitue une contribution à la formulation des mesures de gestion durable des ressources en palissandre.

De nombreux éléments influent sur la croissance d'un arbre notamment son patrimoine génétique, la nature du substrat sur lequel il se développe et son accès aux ressources (lumière, eau ou nutriments) (Assmann 1970). Le patrimoine génétique définit les potentialités intrinsèques de l'arbre et dépend de l'appartenance à une espèce ou à une variété. L'accès d'un arbre aux ressources qui lui sont nécessaires est contrôlé par les phénomènes de compétition. Pour prévoir l'évolution des arbres, les quantifications et les analyses de ces différents facteurs pouvant moduler la croissance sont nécessaires. C'est ainsi que dans cette étude, nous comptons décrire et analyser les effets de l'exploitation et des facteurs du milieu relatifs aux phénomènes de compétition pour les ressources et aux conditions stationnelles sur la dynamique de la croissance de trois espèces de *Dalbergia*.

MATÉRIEL ET MÉTHODES

Matériel végétal

Trois espèces de *Dalbergia* (Fabaceae): *Dalbergia chlorocarpa* R.Vig., *Dalbergia lemurica* Bosser & R.Rabev., *Dal-*

bergia purpurascens Baill., ont été choisies pour cette étude en fonction de leur abondance dans la forêt de Kirindy.

Du point de vue botanique, les trois espèces de *Dalbergia* étudiées possèdent des caractéristiques similaires et communes aux autres espèces de *Dalbergia* qui sont: les feuilles composées imparipennées, les inflorescences généralement terminales portant des fleurs de couleur blanche ou crème parfois teintées de violet, les fruits indéhiscents contenant une à quelques graines et présentant un réseau de nervures au-dessus des graines (Schatz 2001). Elles ont un tronc droit, bien conformé à écorce souvent de teinte claire, grisâtre, crevassée caractéristiques du palissandre (Gueneau & Gueneau 1969). Elles se distinguent entre elles par la dimension des feuilles, le nombre et la forme des folioles. Les feuilles de *Dalbergia chorocarpa* sont longues de 15 à 20 cm et comportent 20 à 40 folioles oblongues et obtuses au sommet. Celles de *Dalbergia lemurica* sont plus petites, ne dépassant pas 10 cm et sont composées de 10 à 20 folioles oblongues et arrondies au sommet. *Dalbergia purpurascens* a des feuilles de 6 à 20 cm de longueur avec 11 à 35 folioles oblongues arrondies à la base. Ces trois espèces de *Dalbergia* sont des arbres de moyenne à grande taille pouvant dépasser 20 m de hauteur, à feuilles caduques. Elles sont présentes dans les forêts décidues sèches de l'Ouest de Madagascar du Nord au Sud et s'installent sur des sols sableux (Bossier & Rabevohitra 2002).

Du point de vue de leur bois, les trois espèces de *Dalbergia* elles sont classées comme du palissandre violet. Elles possèdent des propriétés très similaires et des applications identiques. Leur bois est très dur, moyennement nerveux, durable et résistant (Gueneau 1971). Mais, pour la couleur, le bois de *Dalbergia purpurascens* est plus clair virant au rosé.

Site d'étude

Cette étude s'est focalisée dans un des massifs de forêt dense sèche de Morondava au Sud Ouest de Madagascar compte tenu de l'importance de cette région dans la production de bois d'œuvre. Morondava étant l'une des principales zones productrices de bois d'œuvre à Madagascar avec une production annuelle est estimée à 1000 m³ de bois brut (Leveau & Rakotoaridera 2001). Soixante-dix-huit pour cent de cette production est destiné au marché national notamment celui d'Antananarivo.

La concession forestière de Kirindy est située à 60 km au Nord Est de la ville de Morondava, à environ 20 km de la côte (fig. 1). Elle couvre une superficie de 12 000 ha. Elle est gérée depuis 1978 par le Centre de Formation Professionnelle Forestière. La végétation climacique est la forêt dense sèche caducifoliée appartenant au domaine de l'Ouest de la série à *Dalbergia*, *Commiphora* et *Hildegardia* (Humbert 1955) et à la zone écofloristique occidentale de basse altitude (Faramalala 1995). L'altitude varie de 18 à 40 m environ. Avec des précipitations annuelles de 766 mm, une température moyenne annuelle de 25°C et une longue saison sèche de huit mois, le climat est de type tropical sec (Donque 1975). La forêt de Kirindy repose sur des formations sédimentaires issus de grès du pliocène (Bourgeat 1996). Des sols ferrugineux roux et jaunes occupent la plus grande partie de cette forêt. La forêt de Kirindy est traversée d'Est en Ouest par

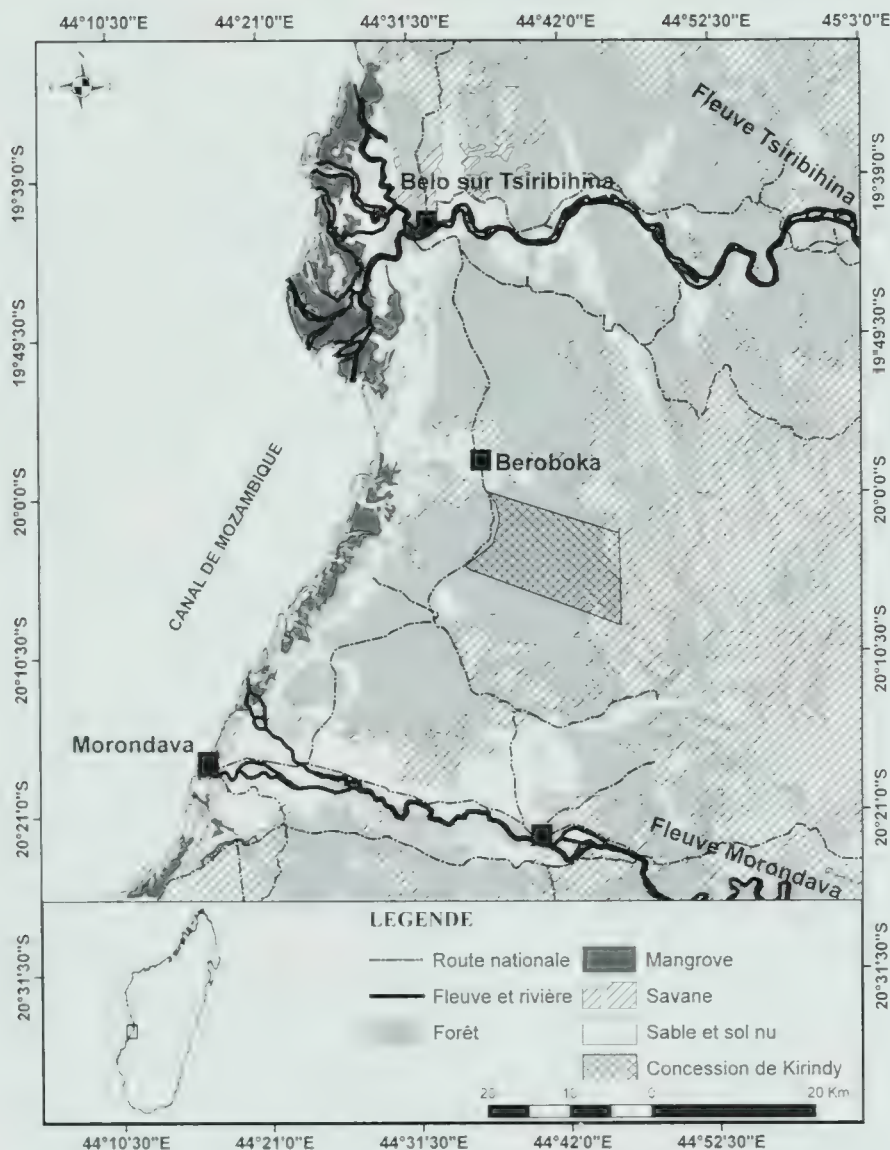


Figure 1 – Localisation de la forêt de Kirindy Morondava au Sud Ouest de Madagascar.

une rivière saisonnière du même nom, qui coule pendant la saison pluvieuse.

La forêt de Kirindy a fait l'objet de travaux d'exploitation et de recherches sylvicoles pendant vingt ans de 1979 à 1999. L'exploitation portait sur plus soixante espèces ligneuses différentes pour des prélèvements de l'ordre de 6 à 20 tiges /ha, soit 4 à 15 m³ (Sorg et al. 2008).

Dispositif d'étude

L'étude de la croissance des populations de trois espèces de *Dalbergia* nécessite des suivis des individus de manière individuelle à intervalles de temps réguliers. L'installation de dispositif permanent de recherche de type parcelle est requise. Les parcelles permanentes doivent permettre d'estimer aussi précisément que possible les paramètres de structure et de dynamique du peuplement. Elles doivent également permettre de mettre en évidence l'impact de l'exploitation forestière sur ces estimations (Picard & Gourlet-Fleury 2008). Une étude préliminaire nous a permis de déterminer l'emplacement et la taille des parcelles permanentes.

Ainsi, pour caractériser les effets de l'exploitation et des conditions stationnelles sur les populations des espèces étudiées, deux parcelles permanentes ont été mises en place:

- parcelle 1 localisée dans un bloc forestier non exploité, situé à proximité de la rivière Kirindy donc à sol plus humide, avec une formation végétale fermée à physionomie apparente intacte.

- parcelle 2 située dans un bloc forestier exploité en 1986 pour un prélèvement de 6,45 m³/ha sur une vingtaine d'espèces, à formation forestière ouverte et à sol plus sec.

La taille des parcelles devra permettre de contenir au moins trente individus mesurables, c'est-à-dire ayant le diamètre minimal de recensement de 5 cm. Une superficie de 9 hectares est à délimiter pour chacun des deux parcelles pour pouvoir disposer de ce minimum d'effectif requis pour les individus à mesurer. Nos deux parcelles d'étude ont une forme carrée de 300 × 300 m.

Collecte et traitement des données

Pour l'étude de la croissance, tous les individus des trois espèces de *Dalbergia* étudiées de diamètre supérieur ou égal à 5 cm à l'intérieur des deux parcelles sont identifiés. Ils ont été marqués et numérotés à la peinture puis positionnés au mètre près. Au total, 711 arbres des trois espèces ont été inventoriés dans les deux parcelles. Dans la parcelle 1, les effectifs des arbres de *D. purpurascens*, *D. chlorocarpa* et *D. lemurica* sont respectivement de 254 arbres, 98 arbres et 174 arbres. Dans la parcelle 2, les arbres sont au nombre de 108 pour *D. purpurascens*, 37 pour *D. chlorocarpa* et 40 pour *D. lemurica*. Leur circonférence à 1,30 m du sol a été mesurée tous les ans pendant trois années consécutives entre 2005 et 2008. La circonférence a été traduite en diamètre en la divisant par π .

Pour exprimer la croissance des espèces étudiées, le paramètre utilisé est l'accroissement courant annuel du diamètre. Dans sa définition originelle, l'accroissement courant annuel d'une grandeur donnée (surface terrière, volume, etc.) représente la moyenne de la production de cette grandeur au cours d'une période précise de la vie du peuplement couvrant une ou plusieurs années (CTFT 1989, Zobi 2002). L'accroissement moyen exprime un rendement global de production et l'accroissement courant exprime un gain ponctuel de production (CTFT 1989). L'accroissement courant annuel du diamètre est la moyenne annuelle de l'accroissement en diamètre des arbres d'un peuplement au cours d'une période de quelques années se terminant au moment de la mesure.

Les différents taux d'accroissement courant annuel ont été déterminés par ajustement linéaire simple de l'évolution du diamètre en fonction du temps. Pour détecter les effets de l'exploitation et des conditions stationnelles sur l'accroissement en diamètre, des comparaisons des accroissements moyens ont été faites à l'aide de l'analyse de variance ANOVA.

La compétition régule l'accès d'un individu aux ressources qui lui sont nécessaires. Elle est l'un des facteurs influençant la croissance des arbres. La quantification des phénomènes de compétition se fait par différents indices représentant les effets exercés par ses voisins sur un arbre dont on cherche à prédire la croissance.

Des travaux d'inventaire des peuplements situés au voisinage des espèces de *Dalbergia* ont été réalisés. Ils ont porté sur le voisinage d'un échantillon de quarante huit pieds par parcelle (dix pieds de *D. chlorocarpa*, douze pieds de *D. lemurica*, 26 pieds de *D. purpurascens*) choisis au hasard. Un dispositif en croix, déduit d'une placette circulaire de 30 m

de rayon, formé par deux bandes d'une longueur de 30 m et d'une largeur de 4 m de direction Nord-Sud et Est-Ouest centré sur chaque pied de *Dalbergia* a été installé. Tous les arbres de diamètre supérieur ou égal à 5 cm présents à l'intérieur des dispositifs ont été inventoriés et identifiés. Leur diamètre à 1,30 m du sol a été mesuré.

Les indices de compétition ont été calculés à partir des données d'inventaire effectué. Il s'agit des indices les plus simples exprimant une densité locale qui sont le nombre total de voisins présents sur le dispositif centré sur l'arbre sujet (NBT) et la surface terrière correspondante (STT) et des indices prenant en compte indirectement le statut social des espèces étudiées. Les indices relatifs au statut social sont le nombre d'arbres dominantes c'est-à-dire de taille supérieure ou égale à celle du sujet échantillonné (NBD) et la surface terrière correspondante (STD).

Pour évaluer les influences des indices de compétition sur la croissance des trois espèces de *Dalbergia*, des tests de corrélation statistiques ont été effectués entre les variables "accroissement courant annuel en diamètre" et "indices de compétition". Les coefficients de corrélation et la probabilité d'avoir un lien entre les variables ont été calculés puis analysés.

RESULTATS

Accroissement annuel du diamètre

Les différents taux d'accroissement courant annuel du diamètre de chacune des trois espèces de *Dalbergia* ont été déterminés dans les deux parcelles. La figure 2 donne les courbes de croissance du diamètre moyen en fonction du temps. L'allure générale de ces courbes est proche de la droite. Les valeurs correspondantes aux équations de ces droites donnent des taux d'accroissement annuel des diamètres variant de 0,12 cm à 0,17 cm. Leurs comparaisons par ANOVA pour tester les effets des facteurs "parcelles" et "espèces" sur les taux d'accroissement indiquent des valeurs de p-value largement supérieures au seuil de signification de 0,05. L'accroissement annuel du diamètre ne diffère pas significativement entre les espèces et entre les parcelles du point de vue statistique.

La croissance des trois espèces de *Dalbergia* qui devrait être stimulée par la lumière dans la parcelle exploitée, étant donné que ces espèces sont héliophiles du moins au stade adulte puisqu'elles occupent la strate supérieure de la forêt, n'a pas semblé bénéficier de l'augmentation de la disponibilité en lumière due à l'ouverture du peuplement par l'exploitation. Les conditions édaphiques défavorables de la

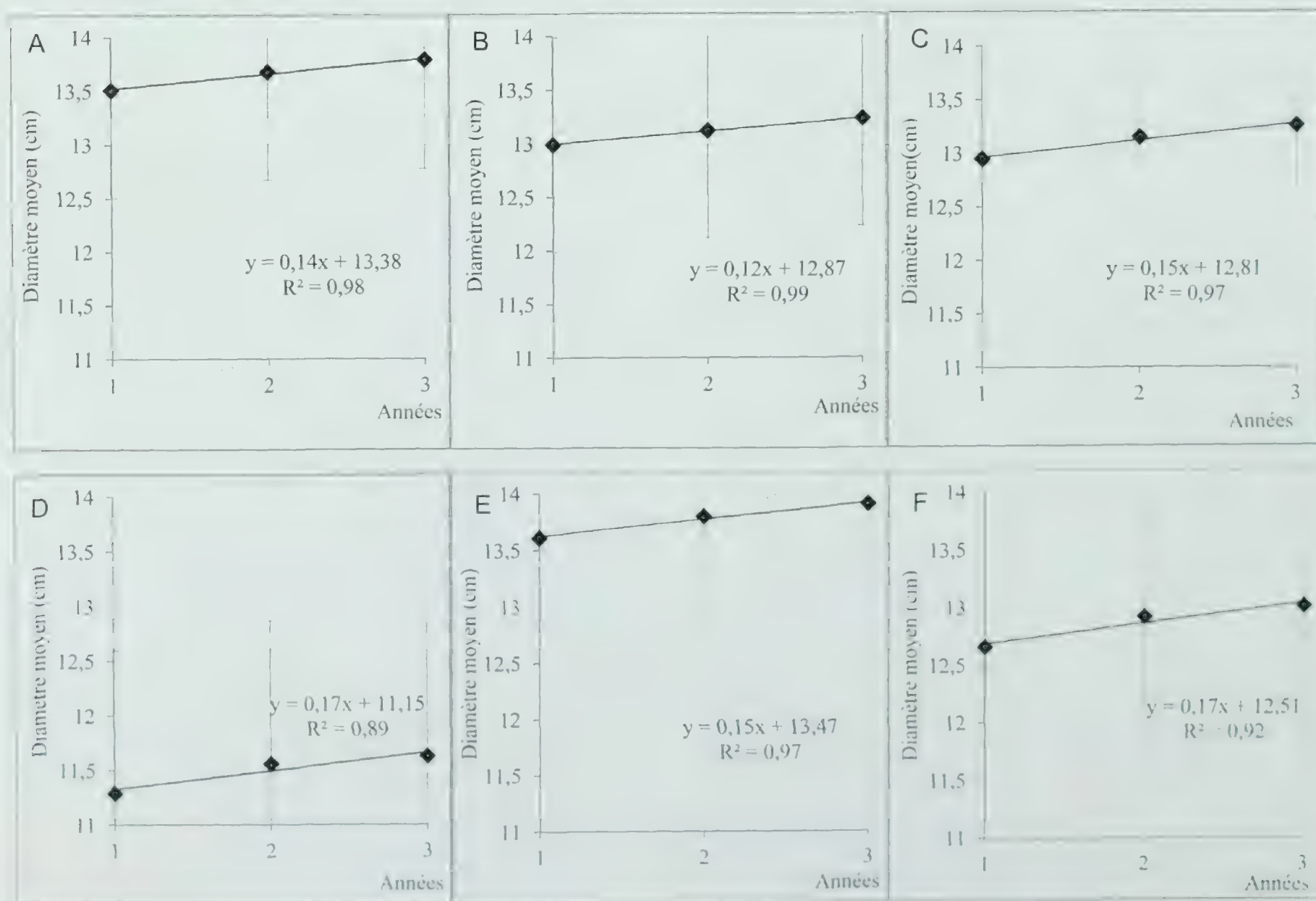


Figure 2 – Evolution du diamètre moyen des trois espèces de *Dalbergia* dans les deux parcelles en fonction du temps: A, *D. chlorocarpa* dans la parcelle 1; B, *D. chlorocarpa* dans la parcelle 2; C, *D. lemurica* dans la parcelle 1; D, *D. lemurica* dans la parcelle 2; E, *D. purpurascens* dans la parcelle 1; F, *D. purpurascens* dans la parcelle 2

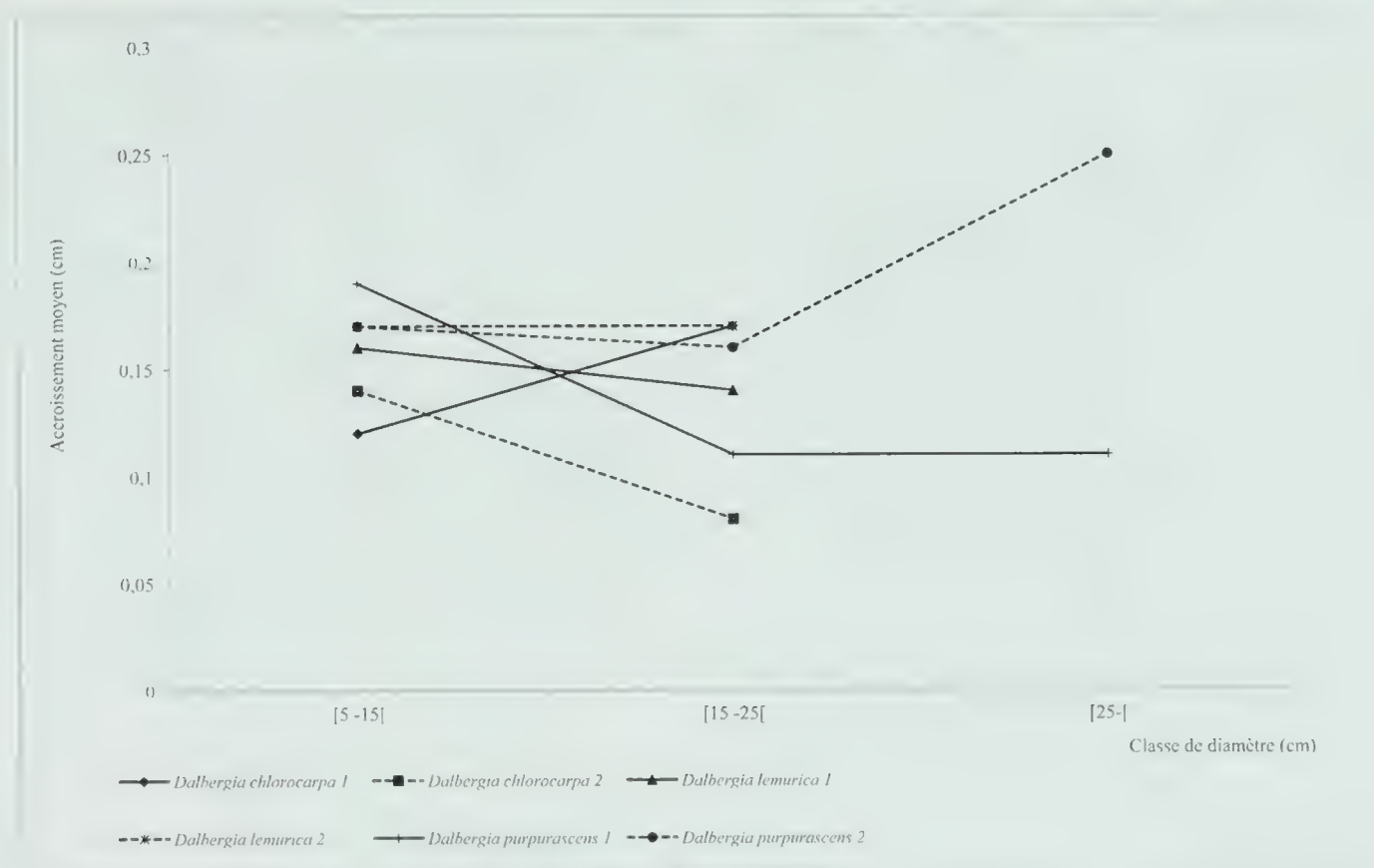


Figure 3 – Accroissement courant annuel en diamètre par espèce, par classe de diamètre et par parcelle.

parcelle 2, sol sec et pauvre en éléments fertiles à cause de l'éloignement de la rivière, ont contrebalancé les effets de la lumière sur la croissance des individus des trois espèces d'où le taux d'accroissement équivalent entre les deux parcelles.

Pour étudier l'influence du diamètre des arbres sur l'accroissement annuel en diamètre des trois espèces étudiées, le taux d'accroissement du diamètre pour chaque classe de diamètre à intervalles de 10 cm a été estimé à partir de la régression linéaire. Les valeurs correspondantes sont fournies par la figure 3.

Les données de la figure 3 montrent que le taux d'accroissement n'est pas proportionnel au diamètre des arbres. Il semble plus élevé pour les individus de *Dalbergia purpurascens* de diamètre inférieur à 15 cm dans la parcelle 1 et de diamètre supérieur à 25 cm dans la parcelle 2. Cependant, pour les individus de diamètre supérieur à 25 cm, le faible effectif des individus mesurés, seulement six arbres, ne permet pas de faire une appréciation statistiquement valable sur ce taux d'accroissement élevé. Les comparaisons statistiques des accroissements annuels en diamètre par l'ANOVA ont donné des valeurs des p-value largement supérieures au seuil de signification de 0,05. L'accroissement courant annuel en diamètre des trois espèces de *Dalbergia* ne diffère pas significativement d'une espèce à une autre, d'une parcelle à une autre et d'une classe de diamètre à une autre.

Phénomènes de compétition pour les ressources

Le taux d'accroissement courant annuel des trois espèces de *Dalbergia* ne diffère pas, entre les parcelles et entre les classes de diamètre, tous les individus des trois espèces dans les deux parcelles ont été regroupés pour l'étude des effets des indices de compétition sur la croissance. Des analyses de corrélations entre les variables: indices de compétition et l'accroissement ont été effectuées. La matrice de corrélation obtenue est représentée dans le tableau 1.

L'examen de cette matrice met en évidence la très forte corrélation entre STT et STD ($r = 0,95$). Les indices les moins corrélés, NBT et NBD avec $r = 0,03$, ont été retenus pour expliquer les liaisons avec l'accroissement moyen en diamètre des espèces de *Dalbergia*. Les coefficients de corrélation observés sont très faibles (avec NBT, $r = 0,025$ et avec NBD, $r = 0,196$). Ils montrent qu'il n'existe aucune relation entre les compétitions pour les ressources et l'accroissement annuel en diamètre. Les tests de corrélation confirment cette absence de lien. Les valeurs de probabilité ou p-value calculées sont largement supérieures au seuil de probabilité de 0,05 (avec NBT: 0,803 et avec NBD: 0,054).

La pression de l'environnement exercée par leurs voisins sur les trois espèces de *Dalbergia* n'affecte pas leur croissance.

Tableau 1 – Corrélation entre les indices de compétition et l'accroissement en diamètre NBT: nombre total de voisins; NBD: nombre de voisins dominants; STT: surface terrière totale; STD: surface terrière des voisins dominants.

	Accroissement moyen	NBT	NBD	STT	STD
Accroissement moyen	1				
NBT	0,02	1			
NBD	0,19	0,03	1		
STT	0,20	0,25	0,10	1	
STD	0,26	0,15	0,24	0,95	1

DISCUSSION

L'accroissement annuel du diamètre des trois espèces de *Dalbergia* est faible, inférieur à 2 mm par an. La croissance lente de ces espèces au stade adulte confirme la théorie de Lamprecht (1981), selon laquelle les bois tropicaux possèdent une croissance initiale rapide en hauteur et en diamètre et en peu de temps, prennent une position dominante puis une phase de croissance réduite commence.

La croissance initiale rapide en hauteur des espèces de *Dalbergia* a été justifiée au cours des travaux de suivi des plantations d'enrichissement dans quelques régions de Madagascar. Les espèces de *Dalbergia* plantées dans la forêt dense sèche d'Antsohihy ont enregistré une croissance en hauteur pouvant atteindre 50 cm/an au cours des six premières années (Andrianjatovo 1983). Dans la forêt humide de moyenne altitude de l'Est située à Sandrangato, la croissance en hauteur des espèces de *Dalbergia* plantées est en moyenne de 34 cm par an (Andrianjatovo 1983). La croissance en diamètre est moins élevée comparée à celle des autres espèces. Pour les espèces de *Commiphora* sp dont on a contrôlé l'accroissement dans la forêt de Kirindy et qui occupent aussi la strate supérieure. L'augmentation du diamètre enregistrée est de 2,5 mm/an (Kayser & Keller 1981).

Les impacts des différents facteurs pouvant influencer sur les potentialités de croissance de trois espèces de *Dalbergia* pris en compte au cours de cette étude n'ont pas été fermement démontrés. Les effets de la lumière et des conditions édaphiques n'ont pas pu être dissociés dans les deux parcelles. La croissance des espèces de *Dalbergia* étudiées n'est pas non plus sensible aux pressions relatives aux compétitions pour les ressources provoquées par les arbres du voisinage. En effet, les indices de compétition utilisés au cours de cette étude connaissent une certaine limite. Ils expliquent seulement l'accès aux ressources en lumière, en eau et en éléments minéraux. La disponibilité de ces ressources constitue également un facteur non négligeable pour expliquer la croissance (Gourlet-Fleury 1998). Il en est de même pour les facteurs intrinsèques liés à la génétique de l'espèce.

Avec un accroissement annuel moyen du diamètre de l'ordre de 0,15 cm/an pour les trois espèces de *Dalbergia*, un arbre de 5 cm de diamètre mettrait environ 167 années pour atteindre 30 cm de diamètre (diamètre de coupe pratiquée pour les bois d'œuvre dans les forêts sèches de l'Ouest de Madagascar) si l'on suppose ce taux constant. Le diamètre minimal d'exploitation légal de 47 cm ne serait atteint qu'au bout de 280 ans. En se référant aux pratiques actuelles de coupe des espèces de *Dalbergia*, où les arbres sont prélevés à partir de 20 cm de diamètre, les arbres de la classe de diamètre compris entre 15 cm et 19 cm mettraient en moyenne 25 ans pour atteindre 20 cm. Pour avoir des simulations de croissance plus fiables, les données de croissance recueillies au cours de cette étude devront être incorporées avec d'autres paramètres liés à la croissance et à la dynamique des populations dans des modèles mathématiques. Elles peuvent donner une certaine idée, certes grossière, sur la durée de rotation des prélèvements pour les espèces de *Dalbergia* qui ne devrait pas être inférieurs à 25 ans.

En définitive, les résultats que nous avons obtenus nous permettent de déduire que la performance en croissance des

trois espèces de *Dalbergia* n'est pas sensible aux perturbations anthropiques et aux conditions environnementales et que la reconstitution du stock exploitable est possible avec une seule rotation de coupe. Les pressions exercées sur les ressources devront être diminuées pour assurer cette reconstitution.

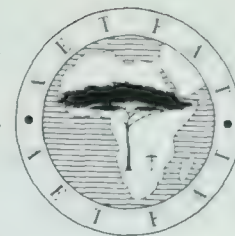
REMERCIEMENTS

Nous remercions le Département de Biologie et Ecologie végétales de la Faculté des Sciences de l'Université d'Antananarivo, l'URP Forêts Biodiversité au CIRAD à Madagascar, l'UR Dynamique des forêts naturelles au CIRAD Montpellier pour leurs appuis techniques et l'IFS pour les financements accordés à la réalisation de cette recherche. Une reconnaissance très méritée revient également aux examinateurs de notre manuscrit.

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- Manuscript received 30 Sep. 2010; accepted in revised version 19 Feb. 2013.
- Communicating Editor: Elmar Robbrecht.



Les plantes médicinales de l'aire protégée de Zahamena (Madagascar) et de ses environs: richesse floristique et endémicité

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Medicinal plants from the Zahamena protected area (Madagascar) and its surroundings: species richness and endemism

Background – There is no exhaustive list of medicinal plants in Madagascar. The latest publication of Rabesa et al. on this subject (1990) suggests that medicinal plants in Madagascar represent only 30% of its flora. Species with wide distribution still dominate the list. There are few data related to medicinal plants within a protected area in Madagascar. The inventory of medicinal plants used by local populations living around the protected area of Zahamena was then conducted.

Methodology – Individual survey was adopted. Pre-established questionnaires were asked to two traditional healers who joined us in the forest. Comparison has been made between medicinal plants of Zahamena, Zahamena flora, medicinal plants of Madagascar, flora of Madagascar and other publications that include pharmacopoeias of Alaotra, Ambongo and Boina.

Key Results – One hundred and five medicinal plant species distributed in 93 genera and 54 families were identified in the protected area of Zahamena. Seventy-seven percent of these species are endemic to Madagascar. Medicinal plants from the protected area of Zahamena are mainly from the most important families from the flora of Madagascar.

Key words – Medicinal plants, endemism, Zahamena, Madagascar.

Contexte – Il n'existe pas encore de liste exhaustive des plantes médicinales malgaches.

La dernière publication de Rabesa et al. à ce sujet (1990) suggère que les plantes médicinales de Madagascar constituent seulement 30% de sa flore. Les espèces à large distribution dominent dans la liste. Les données sur les espèces végétales médicinales à l'intérieur des aires protégées sont minimales. Un inventaire des plantes médicinales utilisées par les populations riveraines de l'aire protégée de Zahamena a donc été entrepris.

Méthodologie – La méthode d'enquête individuelle a été adoptée. Des questionnaires pré établis ont été posés à deux tradipraticiens qui nous ont rejoints dans la forêt. Une comparaison a été effectuée entre les plantes médicinales de Zahamena, la flore de Zahamena, les plantes médicinales de Madagascar, la flore de Madagascar et plusieurs autres publications incluant les pharmacopées de l'Alaotra, de l'Ambongo et du Boina.

Résultats clés – Cent cinq espèces de plantes médicinales réparties dans 93 genres et 54 familles sont recensées dans l'aire protégée de Zahamena. Soixante-dix-sept pour cent de ces espèces sont endémiques de Madagascar. Les plantes médicinales de l'aire protégée de Zahamena font pour la plupart partie des familles les plus importantes dans la flore de Madagascar.

INTRODUCTION

Les plantes peuvent renfermer des principes actifs susceptibles de donner naissance à des médicaments contrôlés et standardisés (De Padua et al. 1999). De ce fait, elles peuvent

constituer une importante source de revenus aussi bien à l'échelle locale qu'à l'échelle internationale.

Pour Madagascar, l'exportation de plantes médicinales à vocation industrielle concerne seulement six espèces et rapportaient 1 189 171 \$ en 1995 (Rasoanaivo 1996). En 1997,

ce chiffre est monté à 1 403 282 \$ (Andriantsiferana & Rajaonson 1998). Flacourt citait déjà l'utilisation de quelques plantes malgaches dans son *Histoire de la grande Isle de Madagascar* (Flacourt 1657).

A partir de la période coloniale, l'intérêt grandissant pour cette zone de l'Océan Indien entraîne la parution de nombreux ouvrages sur les plantes utiles, et ceci dès le début du XIX^e siècle. Les travaux concernant l'ethnobotanique se sont encore multipliés après la création de l'Institut Colonial de Marseille en 1893.

En 1901, la première thèse en ethnobotanique concernant Madagascar est soutenue par Ramisiray.

En 1903, Heckel a publié 'les plantes médicinales et toxiques de Madagascar' dans les *Annales du Musée Colonial de Marseille*. Ce catalogue cite alphabétiquement les noms scientifiques et les noms malgaches des plantes médicinales et toxiques avec leurs emplois, ainsi que leurs indications géographiques. Sept ans plus tard, le même auteur a édité un volume élargi aux autres plantes utiles de Madagascar (Heckel 1910). Quarante ans plus tard, Decary (1946) effectuait une synthèse bibliographique des plantes utiles de Madagascar. Celle-ci concerne les plantes utiles autres que les plantes médicinales déjà publiées avant cette date.

En 1976, le Département 'Plantes Médicinales' de l'ORSTOM a été intégré dans le Centre National d'Application de Recherches Pharmaceutiques (CNARP, ex CNRP) au sein du Département d'Ethnobotanique et de Botanique. Cette institution de recherche a pu publier la *Pharmacopée de l'Alaotra* (Rabesa 1986) et les *Pharmacopées de l'Ambongo et du Boïna* (Rakotobe et al. 1993).

En 1979, la Librairie de Madagascar publie le *Précis de matière médicale Malgache* compilé par Pierre Boiteau. Ce livre sera ré-édité en 1986 par l'Agence de Coopération Culturelle et Technique. Ce travail est complété par sa fille Lucile Allorge qui élabore en 1998 un CD-Rom intitulé *Plantes médicinales de Madagascar*.

A l'Université d'Antananarivo, le Département de Biologie et Ecologie Végétales (Faculté des Sciences d'Antananarivo) et le Département des Eaux et Forêts (Ecole Supérieure en Sciences Agronomiques), en collaboration avec des ONG et des institutions nationales ont fait de nombreuses recherches en vue de la conservation et de la gestion durable. Néanmoins, l'étude des plantes utiles reste encore insuffisante par rapport aux travaux d'inventaire botanique, écologique et systématique.

Depuis l'année 2003, le projet *Plant Resources of Tropical Africa* (PROTA) a démarré au sein du Parc Botanique et Zoologique de Tsimbazaza (PBZT). Ce projet a pour objectif de faire la synthèse des informations dispersées sur environ 7 000 plantes utiles de l'Afrique tropicale, et de fournir un large accès à ces informations par le moyen de bases de données sur le web, de livres, de CD-Roms et de produits spéciaux. Durant sa première phase d'activité, le projet a permis de publier différents tomes de *Ressources végétales d'Afrique tropicale* concernant les céréales et légumes secs, les légumes, les colorants et tanins, les bois d'œuvre, les oléagineux et les plantes médicinales (Grubben & Denton 2004, Brink & Belay 2006, Van de Vossen & Mkamilo 2007, Luppe et al. 2008, Schmelzer & Gurib-Fakim 2008).

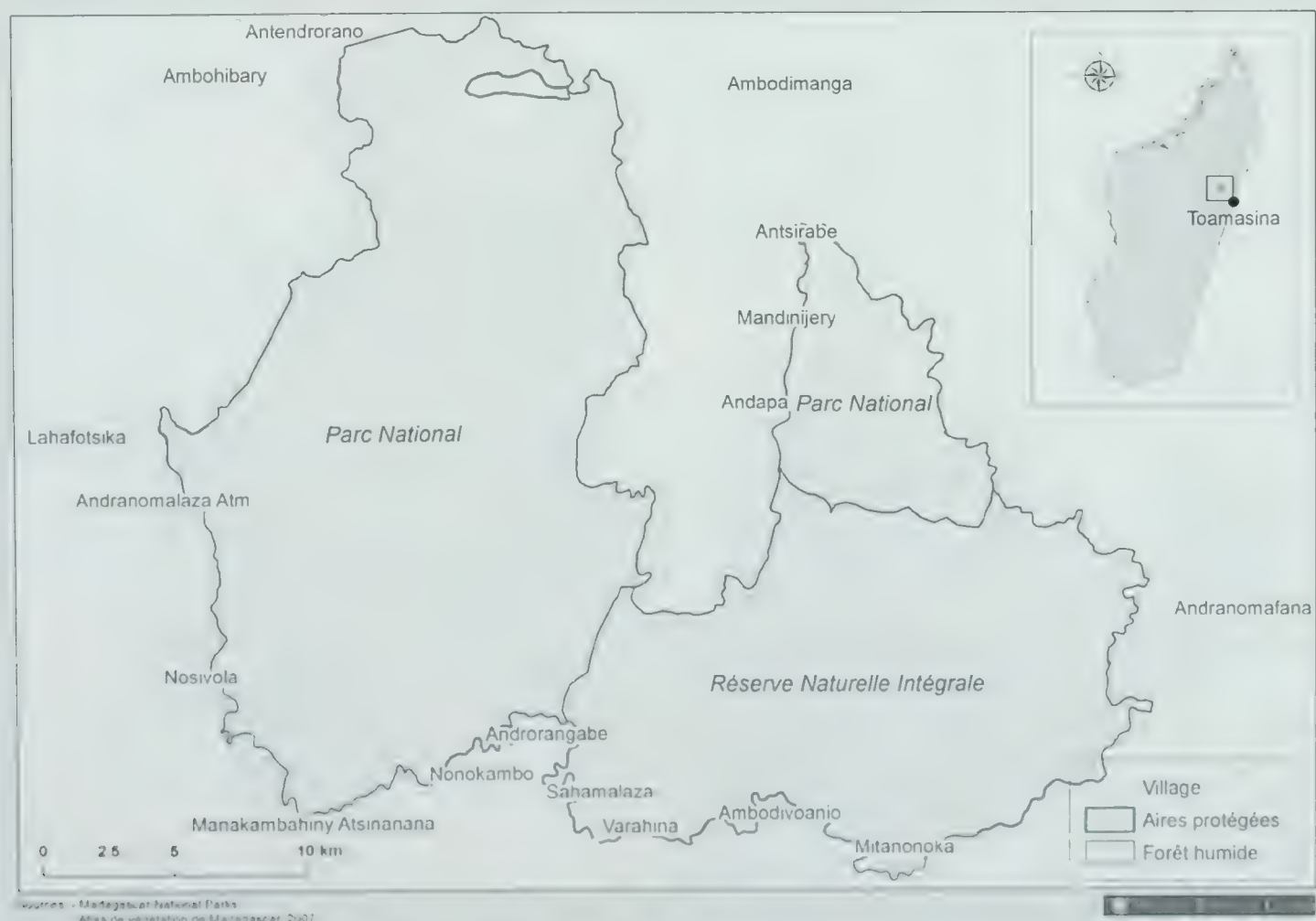


Figure 1 - Carte de localisation de l'aire protégée de Zahamena.

Cependant, il n'existe pas encore de liste exhaustive des plantes médicinales malgaches. On estime que Madagascar compte environ 12 000 espèces de plantes vasculaires (Koechlin et al. 1974) dont seulement 30% seraient médicinales, parmi lesquelles dominent les espèces à large distribution (Rabesa et al. 1990). Les données des espèces végétales médicinales à l'intérieur des aires protégées sont encore minimales.

Ainsi, l'inventaire des plantes médicinales utilisées par les populations autour des aires protégées de Zahamena a été effectué durant les années 2000 à 2003.

Il semblerait que le déplacement des informateurs dans la forêt permet de recueillir des indications sur des espèces endémiques, alors que l'enquête dans les villages fait ressortir les informations sur les espèces à large distribution.

Les principaux objectifs de l'enquête étaient:

- connaître les espèces médicinales de l'aire protégée de Zahamena,
- analyser ses caractéristiques floristiques,
- étoffer la liste des plantes médicinales de Madagascar,
- évaluer la pertinence de notre méthode d'enquête et d'inventaire des plantes médicinales.

METHODES

Site d'étude

La forêt de Zahamena est localisée dans la partie orientale de Madagascar (fig. 1). Cette forêt est composée du Parc National de Zahamena et de la Réserve Naturelle Intégrale de Zahamena. La superficie totale atteint 64 400 ha. Des forêts communautaires entourent l'aire protégée.

La végétation est caractéristique des forêts humides de basse et de moyenne altitudes (Koechlin et al. 1974). Par contraste, la zone périphérique est occupée en grande partie par des savanes, des plantations d'*Eucalyptus* et des formations forestières secondaires.

La population riveraine est constituée du clan Sihanaka sur le versant Ouest et du clan Betsimisaraka sur le versant Est.

Collecte et analyse des données

Après avoir expliqué les objectifs de nos recherches, deux tradipraticiens, l'un venant du clan Sihanaka et l'autre venant du clan Betsimisaraka ont accepté de participer à notre enquête. Ils sont très connus dans leurs régions respectives et possèdent d'amples connaissances sur les plantes et leurs usages empiriques.

La récolte des données a été faite entre 2000 et 2003. Chaque tradipraticien nous a accompagné dans la forêt et nous a fait part de ses connaissances tout au long des déplacements, la personne enquêtée énumérant l'utilisation des espèces rencontrées (Rao & Hajra 1987, Cunningham 2001). Les renseignements donnés par l'informateur ont été enregistrés textuellement (Rao & Hajra 1987, Cunningham 2001). Pour chaque espèce, le lieu de récolte a été géolocalisé. Suivant la méthodologie de Rao & Hajra (1987) et de Cunningham (2001), les spécimens d'herbiers ont été pres-

sés, séchés et déposés dans l'herbier du CNARP ainsi que dans les herbiers aux acronymes suivants: TAN, TEF, P, MO; cette méthode permettant d'authentifier l'information et de conserver plusieurs échantillons de référence. Les plantes ont été identifiées par l'auteur dans l'herbier du Parc Botanique et Zoologique de Tsimbazaza (TAN), l'herbier de la Direction de Recherche Forestière et Piscicole (TEF) et l'herbier du Centre National d'Application de Recherches Pharmaceutiques (CNARP) à Madagascar en utilisant les herbiers et les publications concernant la flore de Madagascar.

Une base des données de la flore médicinale de Zahamena a été créée, en comparant les informations recueillies au cours de l'enquête avec la flore de Zahamena (Centre National d'Application de Recherches Pharmaceutiques, Conservation International Madagascar & Missouri Botanical Garden 2002), la pharmacopée de l'Alaotra (Rabesa 1986) et les pharmacopées de l'Ambongo et du Boina (Rakotobe et al. 1993). Certaines données ont été complétées grâce à la documentation sur la flore médicinale de Madagascar (Rabesa et al. 1990) et celle contenue dans la *Flore de Madagascar et des Comores* (Humbert & Leroy 1936-présent).

Un tableau Excel compilant les informations a été utilisé pour trier les données, déterminer les proportions et dessiner les graphiques.

Le nombre d'espèces endémiques a été comparé entre la flore médicinale de Zahamena et la flore de Madagascar, de même qu'avec des ressources provenant de diverses publications (pharmacopée de l'Alaotra, pharmacopées de l'Ambongo et du Boina, et flore de Madagascar).

RÉSULTATS

Les plantes inventoriées sont listées par ordre alphabétique des noms scientifiques, suivi du nom de la famille, de l'endémicité, du nom local, de l'utilisation locale et du mode de préparation (appendice électronique).

De la préparation des médicaments aux indications

Les parties de plantes utilisées – La fréquence d'utilisation des différentes parties des plantes est résumée par ordre décroissant (fig. 2).



Figure 2 – Histogramme de fréquence d'utilisation des différentes parties des plantes.

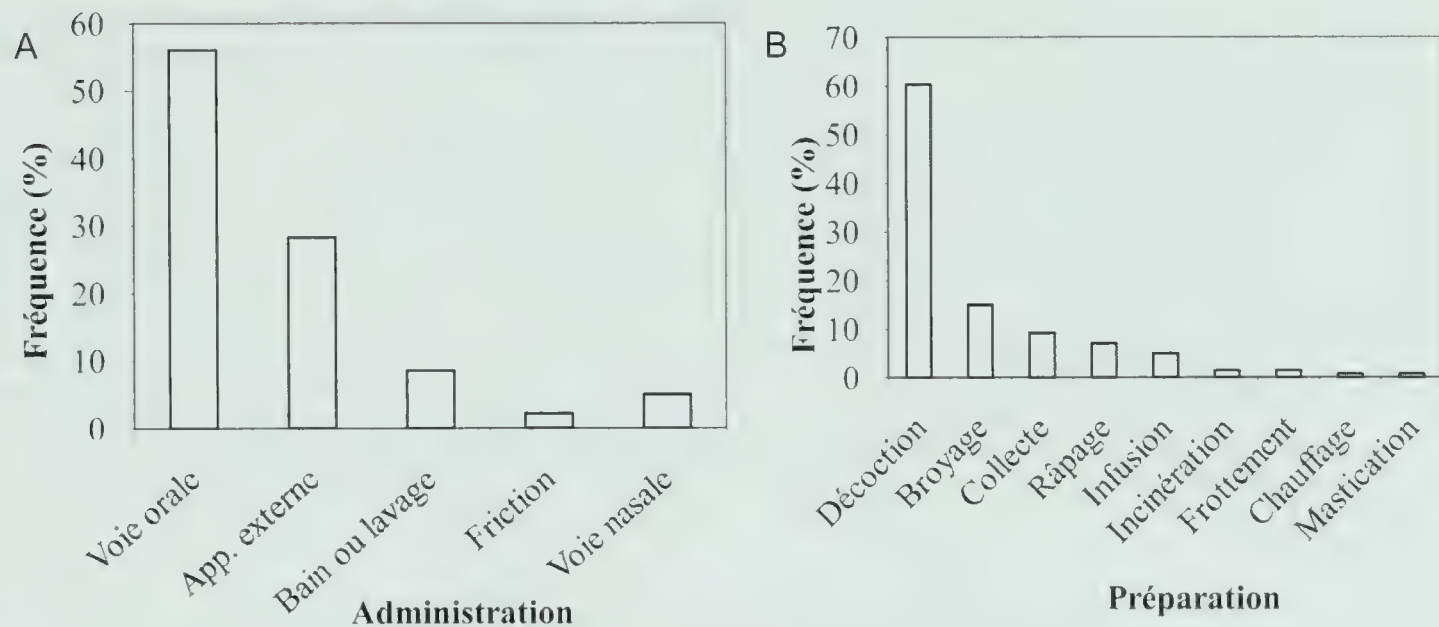


Figure 3 – Histogramme de fréquence: A, des types d'administration; B, des préparations.

Cet histogramme montre que les tradipraticiens font usage de plusieurs sortes d'organes végétaux. Cependant, les feuilles sont les plus fréquemment prescrites (41%), puis suivent l'écorce (18%) et les racines (10%) pour préparer les remèdes. La cueillette de ces deux dernières est néfaste pour la plante. Ainsi, presque tous les grands pieds de *Pentachlaena orientalis* Capuron poussant au bord de la piste traversant l'aire protégée sont morts. Les villageois prélèvent des écorces de cette espèce lors de leur passage, conduisant à l'étiollement des plantes. L'usage des tiges, des fruits, des exsudats et des rameaux feuillés est modéré. Seules les plantes herbacées sont utilisées dans leur intégralité (feuilles et tiges). Les graines sont rarement prescrites. La majorité des parties prélevées sont en général préparées à l'état frais et les tradipraticiens ne constituent pas de réserves.

La préparation et l'administration des médicaments – La fréquence des types d'administration et les préparations des plantes avant le traitement des malades sont représentées sous forme d'histogrammes (fig. 3A & B).

Ces derniers indiquent que le mode de préparation principal est la décoction (60%) suivi du broyage (15%). L'administration se fait surtout par voie orale (56%).

Principales affections – Le tableau 1 recense les dix maladies les plus citées par les tradipraticiens, ainsi que la

fréquence d'utilisation des espèces servant à traiter ces maladies.

Richesse en flore médicinale

Les familles les mieux représentées sont par ordre d'importance: Asteraceae (onze espèces), Rubiaceae (dix espèces), Euphorbiaceae (sept espèces), Myrsinaceae (cinq espèces), Melastomataceae et Clusiaceae (quatre espèces chacune). Les genres les plus fréquents sont *Helichrysum* et *Oncostemum* (trois espèces chacun).

Les dix premières familles les mieux représentées de la flore de Madagascar, des plantes médicinales de Madagascar, de la flore des Aires protégées de Zahamena, et des plantes médicinales de l'Alaotra sont comparées avec les dix premières familles les mieux représentées de la flore médicinale des aires protégées de Zahamena (tableau 2).

Ce tableau montre que:

- 6 familles sont communes à la flore de Madagascar et à la flore médicinale de l'aire protégée de Zahamena (Apocynaceae, Asteraceae, Euphorbiaceae, Melastomataceae, Rubiaceae et Sterculiaceae)
- 6 familles de la flore de l'aire protégée de Zahamena se retrouvent dans sa flore médicinale (Apocynaceae, Asteraceae, Clusiaceae, Euphorbiaceae, Myrsinaceae et Rubiaceae)
- la moitié des dix familles les plus représentées dans la flore médicinale de Madagascar sont présentes dans la liste des dix familles les plus représentées de la flore médicinale de Zahamena (Apocynaceae, Asteraceae, Euphorbiaceae, Moraceae, Rubiaceae)
- la composition de la flore médicinale de Zahamena est globalement différente de celle de la flore médicinale de l'Alaotra (seulement 3 familles en commun: Asteraceae, Euphorbiaceae et Moraceae)
- une famille de la flore médicinale de Zahamena ne se retrouve dans aucune du 'top ten' des familles des flores mentionnées: il s'agit de la famille des Menispermaceae.

Globalement, on peut dire que, concernant les dix familles les plus représentées, la composition de la flore médicinale de l'aire protégée de Zahamena semble plus proche

Tableau 1 – Fréquence des espèces servant à traiter dix premières maladies.

Indications thérapeutiques	Fréquence
Plaie	12,14
MST	7,86
Diarrhée et vomissement	7,86
Toux	5,71
Gale	5,71
Paludisme	4,29
Marasme	3,57
Furuncle	3,57
Aphrodisiaque	3,57
Jaunisse	2,86

Tableau 2 – Comparaison des dix premières familles les mieux représentées dans la flore médicinale de l’aire protégée de Zahamena avec les dix premières familles les mieux représentées dans la flore de Madagascar, la flore médicinale de Madagascar, la flore de l’aire protégée de Zahamena, et la flore des plantes médicinales de l’Alaotra.

Flore de Madagascar	Flore médicinale de Madagascar	Flore de l’aire protégée de Zahamena	Flore médicinale de l’Alaotra	Flore médicinale de Zahamena
Acanthaceae	Apocynaceae	Apocynaceae	Amaranthaceae	Apocynaceae
Apocynaceae	Asclepiadaceae	Aralicaeae	Asclepiadaceae	Asteraceae
Asteraceae	Asteraceae	Asteraceae	Asteraceae	Clusiaceae
Euphorbiaceae	Euphorbiaceae	Clusiaceae	Cucurbitaceae	Euphorbiaceae
Fabaceae	Fabaceae	Euphorbiaceae	Euphorbiaceae	Melastomatacaeae
Lamiaceae	Lamiaceae	Fabaceae	Fabaceae	Menispermaceae
Melastomatacaeae	Moraceae	Lauraceae	Lamiaceae	Moraceae
Orchidaceae	Poaceae	Myrsinaceae	Moraceae	Myrsinaceae
Rubiaceae	Rubiaceae	Rubiaceae	Poaceae	Rubiaceae
Sterculiaceae	Rutaceae	Sapindaceae	Solanaceae	Sterculiaceae

Tableau 3 - Comparaison du nombre d’espèces médicinales de Zahamena avec celui de Madagascar, de l’Alaotra, et avec la richesse spécifique de l’aire protégée de Zahamena.

	Plantes médicinales de Zahamena	Flore de l’aire protégée de Zahamena	Pharmacopée de l’Alaotra	Pharmacopées de l’Ambogo et du Boina	Plantes médicinales de Madagascar
Nombre d’espèces	104	740	252	300	2777
Espèces endémiques	76,92%	79,59%	33,73%	70%	39%
Méthodologie employée	Tradipraticiens se déplacent dans la forêt	Rapport sur l’utilisation de la biodiversité à Madagascar et au Suriname	Enquêtes effectuées dans les villages	Tradipraticiens se déplacent dans la forêt	Synthèse bibliographique

de la composition de la flore générale de Madagascar et de la flore générale de l’aire protégée que des flores médicinales citées (Madagascar, Alaotra). Deux familles (Fabaceae et Lamiaceae) semblent être peu utilisées par les tradipraticiens de l’aire protégée de Zahamena, contrairement à d’autres pratiques médicinales dans l’île.

Les différentes formes biologiques des espèces rencontrées sont représentées à l’aide d’un diagramme (fig. 4). Ce diagramme montre que les formes biologiques dominantes sont les arbres et les arbustes (62%). Les espèces herbacées ne représentent que 15%.

Richesse et endémisme spécifique

Le nombre d’espèces médicinales de l’aire protégée de Zahamena est très faible (tableau 3). Ces espèces constituent environ le septième de sa flore vasculaire, et la moitié des espèces rencontrées dans la pharmacopée de l’Alaotra.

Pour l’ensemble de l’île, les plantes médicinales occupent environ le tiers de sa flore. Le chiffre très bas recueilli lors de l’enquête dans l’aire protégée de Zahamena peut être expliqué par le nombre insuffisant d’informateurs. Notons qu’une vingtaine de tradipraticiens ont participé à l’élaboration de la pharmacopée de l’Alaotra.

On remarque également que le pourcentage d’espèces endémiques est très élevé (76,92%) pour la flore médicinale

de Zahamena, et qu’il se rapproche du taux d’endémisme constaté dans les pharmacopées de l’Ambogo et du Boina (70%). Cet endémisme fort est également caractéristique de la flore générale de Zahamena.

Ceci mène à souligner l’influence de l’approche méthodologique choisie sur la collecte de données concernant les espèces médicinales endémiques. En effet, les enquêtes cantonnées aux abords des villages vont surtout révéler les usages des espèces à large distribution (voir le pourcentage d’espèces endémiques de la pharmacopée de l’Alaotra qui n’est que de 33,73%).



Figure 4 – Diagramme des formes biologiques

En forêt, où les espèces médicinales endémiques sont abondantes, les tradipraticiens se souviennent directement de l'emploi médicinal dès qu'ils rencontrent l'espèce.

DISCUSSION ET CONCLUSION

L'aire protégée de Zahamena est riche en plantes médicinales. Les tradipraticiens gardent encore de bonnes connaissances sur l'utilisation des plantes indigènes et sur le traitement des maladies. Ainsi, nos résultats montrent que 104 espèces végétales ont été indiquées pour traiter 35 types de maladies. Les tradipraticiens connaissent surtout les plantes servant à traiter les maladies fréquentes dans leur région.

En toute logique, à Madagascar (Rabesa 1986, Rabesa et al. 1990, Rakotobe et al. 1993) et en Afrique (Yineger et al. 2008), les parties aériennes de la plante sont les plus fréquemment utilisées puisqu'elles sont directement disponibles pour la récolte, et généralement accessibles toute l'année. La décoction est un mode de préparation fréquemment rencontré, et la plupart des remèdes sont administrés par voie orale.

Les résultats de cette étude montrent également une endémicité spécifique très élevée par rapport aux autres études ethnomédicinales de Madagascar. Cette endémicité de la flore médicinale semble aller de pair avec celui de la flore. Selon les auteurs, l'endémicité varie de 81% (Humbert 1956) pour la flore vasculaire à 96% (Schatz 2001) pour les arbres et les arbustes.

Quant aux plantes médicinales, les analyses des données ethnobotaniques disponibles à Madagascar avant 1982 faites par Andriantsiferana suggèrent que la médecine traditionnelle malgache a surtout utilisé les espèces communément répandues dans le monde tropical, facilement accessibles à la population, poussant à proximité des habitations, malgré la forte endémicité de la flore Malgache. Ceci vient du fait que la plupart des informations sont recueillies aux abords des grands axes routiers (Andriantsiferana 1982). Les données publiées par Rabesa et ses équipes en 1990 n'enregistrent qu'un pourcentage de 39% d'espèces médicinales endémiques. Parmi les 43 espèces médicinales inventoriées par Novy, en 1997 dans la région d'Analanjorofo, douze espèces seulement sont endémiques (Novy 1997). Les analyses de l'endémicité spécifique de la pharmacopée de l'Alaotra (Rabesa 1986) montrent une valeur très faible (33%).

Par contre, dans les pharmacopées de l'Ambongo et du Boïna (Rakotobe et al. 1993), l'endémicité spécifique est élevée (70%); car, d'abord, les tradipraticiens vont dans la forêt ensemble avec les enquêteurs, et en suite, les enquêtes sont menés jusqu'aux villages aux alentours des forêts.

Bien que Zahamena soit situé entre l'Alaotra et l'Analanjorofo, nous pensons pouvoir encore inventorier un grand nombre d'espèces médicinales endémiques.

Pour bien inventorier et valoriser les plantes médicinales autochtones et endémiques à Madagascar, il est nécessaire de faire les enquêtes chez les populations autour des forêts, loin des grands axes routiers et les tradipraticiens sont rendus dans la forêt pendant la collecte des informations.

Ainsi, le déplacement des informateurs ou des tradipraticiens dans l'aire protégée durant l'enquête est fortement

recommandé pour bien inventorier et valoriser les plantes médicinales autochtones et endémiques.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible au format pdf sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> > SBB50 > dossier 536) et consiste en une liste des plantes médicinales de l'aire protégée de Zahamena.

REMERCIEMENTS

Nous adressons ici nos vifs remerciements à Madagascar National Park et au Ministère de l'environnement et des forêts pour la délivrance de l'autorisation de recherche, aux populations riveraines pour leur accueil chaleureux, à M.Raminosoa Tantely, Sigiste du Missouri Botanical Garden pour l'élaboration de la carte de localisation du site d'étude, à M.Ratovoson Fidisoa, M. Andrianjafy Mamisoa, Razafintsalama Lalao J., Botaniste du Missouri Botanical Garden, par leurs aides aussi bien au laboratoire que sur le terrain, à M.Rakotondrafara Andriamalala, M.Rakotondrajaona Roland, Randrianasolo Solofo Sennen, Botaniste du CNARP, par leurs assistances sur la collecte et la gestion des données, et au Dr. Rasamison Vincent, Chimiste, pour la traduction en Anglais. Nous n'oublions pas de remercier Rapaolomananjara Justin et Doany, tradipraticiens, et de leur dédier le présent travail.

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Manuscript received 29 Sep. 2010; accepted in revised version 11 May 2011.

Communicating Editor: Rainer Bussmann.



Les ignames cultivées (*Dioscorea alata* - Dioscoreaceae) des régions occidentales malgaches: ethnobotanique, morphologie et diversité génétique

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The cultivated yams (*Dioscorea alata* - Dioscoreaceae) of the west of Madagascar: ethnobotany, morphology and genetic diversity

Context – The cultivated yams which constituted the staple food of the first Malagasy before the 18th century are at the moment neglected for the benefit of rice, manioc and sweet potato. They are represented in Madagascar by two species, *D. alata* and *D. esculenta*. An investigation on the cultivated yams was led in the western regions of Madagascar.

Methodology – Ethnobotanic studies were made in the region of Menabe and in the National Park of Ankarafantsika (region of Boina) to supply the list of the forms of cultivated yams, their uses as well as their system of culture. A morphological study was led to know the characteristics of every form. Then, the distinction between the forms of yam was verified by statistical analyses (tests ANOVA and of Newman-Keuls) and by genetic analysis based on the use of four combinations primer-restriction enzyme on the chloroplastic genome according to the method RFLP-PCR.

Results – According to the farmers' perception, there are five forms of *D. alata*. Tubers, bulbils and leaves are consumed by the local populations. Their cultivation system is qualified vegetable culture or cultivated among other crops. Five forms are inventoried and distinguished themselves by the morphology of their stems, leaves, tubers, bulbils and by the presence or the absence of flowers. Two different groups of *D. alata* were revealed by the ANOVA test and the Newman-Keuls test. However, the molecular studies did not allow to confirm the results of the statistical analyses.

Conclusion – At this stage of our research, the evidence of the presence of several *D. alata* cultivars in the west of Madagascar is not confirmed. The use of other molecular markers is necessary to refine our results.

Key words – Cultivation, *Dioscorea alata*, genetic diversity, morphology, RFLP-PCR, uses.

Contexte – Les ignames cultivées qui constituaient l'alimentation de base des premiers malgaches avant le 18^{ème} siècle sont actuellement des ressources négligées au profit du riz, du manioc et de la patate douce. Elles sont représentées à Madagascar par deux espèces, *D. alata* et *D. esculenta*. Une investigation sur les ignames cultivées a été menée dans les régions occidentales malgaches.

Méthodologie – Des enquêtes ethnobotaniques ont été effectuées dans la région du Menabe et dans le Parc National d'Ankarafantsika de la région de Boina pour fournir la liste des formes d'ignames cultivées, leur utilisation ainsi que leur système de culture. Une étude morphologique a été conduite pour savoir les caractéristiques de chaque forme. La distinction entre les formes d'igname est ensuite vérifiée par des analyses statistiques (tests ANOVA et de Newman-Keuls) et une analyse génétique basée sur l'utilisation de quatre systèmes amorce-enzyme de restriction de l'ADN chloroplastique selon la méthode RFLP-PCR.

Résultats – Selon la perception des paysans, il existe cinq formes de *D. alata*. Les tubercules ainsi que les bulbilles et les feuilles sont consommées par les populations locales. Elles sont cultivées selon le système de végéticulture ou mélangées à d'autres cultures. Les cinq formes inventoriées se distinguent par la morphologie de leurs tiges, feuilles, tubercules, bulbilles et par la présence ou l'absence de fleurs. L'existence de deux groupes distincts de *D. alata* a été mise en évidence par les tests ANOVA et de Newman-Keuls. Cependant, les études moléculaires n'ont pas permis de confirmer les résultats des études morphométriques.

Conclusion – Au stade de nos recherches, nous ne pouvons pas dire qu'il existe plusieurs cultivars de *D. alata* dans l'ouest de Madagascar. Le recours à d'autres marqueurs moléculaires est nécessaire pour affiner nos résultats.

INTRODUCTION

Les ignames ou *Dioscorea* (Dioscoreaceae) sont des plantes, cultivées ou sauvages des pays tropicaux (Asie, Afrique et Amérique). Les espèces cultivées, représentées par *D. alata* et *D. esculenta* originaires de l'Asie et/ou du Pacifique, étaient cultivées avant le 18^{ème} siècle par les malgaches (Perrier de la Bâthie 1925). A cette époque, elles constituaient l'alimentation de base des premiers malgaches ayant peuplé l'île mais elles ont été supplantées par le riz et d'autres plantes à racines et tubercules (Raison 1992). Ainsi, l'igname est tombée en désuétude au profit de ces autres ressources dont la culture s'avérait être plus facile. Or, il a été démontré scientifiquement que les ignames sont plus intéressantes, du point de vue nutritionnel et digestibilité, que les tubercules habituels (DBFA & DBEV 2005).

Le travail présenté dans ce papier a été élaboré dans le cadre du projet Valorisation de l'agrobiodiversité des ignames malgaches du programme CORUS II (Coopération pour la Recherche Universitaire et Scientifique) dont le principal objectif est de valoriser par la recherche les ignames cultivées de Madagascar afin de contribuer à terme à une meilleure sécurisation alimentaire et de soutenir une diversification de l'alimentation très centrée sur le riz. En effet, la connaissance des cultivars intéressants chez les espèces cultivées de Madagascar et la maîtrise de leurs techniques culturelles pourront encourager leur culture et leur production en grande quantité.

MATERIELS ET METHODES

Zone d'étude

L'étude a été réalisée dans la région occidentale de Madagascar. Les ignames y occupent une place importante dans la vie de la population locale. Les études ont été réalisées dans la région du Menabe (Beroboka, d'Andranomena et de Mahabo) et la région du Boeny, dans le MNP (Madagascar National Parks) d'Ankarafantsika (appendice électronique: fig. 1). Dans ces deux régions, des menaces et pressions sur les espèces endémiques malgaches de *Dioscorea* sauvages ont été identifiées (Rajaonah 2004, Rakotondratsimba 2008). La collecte abusive des tubercules ont menacé la pérennité de ces espèces. Après chaque récolte, les trous sont abandonnés et les cornes de tubercules n'y sont pas remises pour qu'ils puissent régénérer l'année suivante. De ce fait, la connaissance des cultivars intéressants chez les espèces cultivées de la région occidentale et la maîtrise de leurs techniques culturelles pourront encourager leur culture et leur production en grande quantité. Ceci permettra à la fois de rehausser la valeur des ignames cultivées et de diminuer les pressions qui s'exercent sur les ignames sauvages en vue de préserver et de conserver la diversité des ignames endémiques.

Matériel végétal

Cette étude concerne l'espèce *Dioscorea alata*, seule espèce d'igname cultivée dans la région de Boeny et de Menabe. C'est une plante lianescente dont les feuilles sont opposées ou alternes, plus ou moins cordiformes et la tige est quadrangulaire ailée. Actuellement, il existe plus de 35 noms ver-

naculaires malgaches pour *D. alata* et plus d'une vingtaine de formes différentes (Jeannoda com. pers.).

METHODOLOGIE

Enquêtes ethnobotaniques

Les enquêtes ont été menées individuellement ou par groupe ("focus groupe"). Ces enquêtes ont permis surtout d'enrichir les informations tout en faisant participer chaque personne enquêtée par des échanges d'idées sur les ignames et leur culture. Diverses questions ont été formulées de manière à obtenir le maximum d'informations sur les formes d'ignames cultivées et leur clé de détermination, la perception paysanne de la biologie de ces ignames, leurs systèmes de culture et leurs utilisations. Ces enquêtes ont été réalisées auprès de 35 hommes et vingt femmes cultivateurs d'igname et auprès de dix enfants.

Etudes morphologiques

Chaque forme de *D. alata* recensée sur le terrain a été décrite. La morphologie de l'appareil végétatif et de l'appareil reproducteur a été notée par le biais des observations à l'œil nu ou à la loupe binoculaire.

Etudes morphométriques

Sur trois à sept échantillons de chaque forme de *D. alata* récoltés sur terrain, des mesures ont été prises sur les tubercules, les tiges et feuilles matures se situant entre le sixième et le dixième nœud. Douze paramètres ont été mesurés: longueur de l'entre-nœud, diamètre de l'entre-nœud, longueur du pétiole, largeur du sinus, largeur de l'auricule, longueur de l'auricule, longueur du limbe, largeur du limbe, longueur de l'acumen, longueur du tubercule, diamètre du tubercule et poids du tubercule.

Ces données ont ensuite été traitées par l'analyse de variance (ANOVA) et par le test de Newman-Keuls afin de dégager la différence entre les formes de *D. alata*.

Diversité génétique

La technique CAPS (Cleaved Amplified Polymorphic Sequence, Konieczny & Ausubel 1993) ou RFLP-PCR (Restriction Fragment Length Polymorphism -Polymerase Chain Reaction, Deng 1988) a été utilisée pour vérifier l'existence d'une diversité génétique ou de polymorphisme entre les formes d'ignames cultivées recensées. Pour chaque forme de *D. alata* recensée sur terrain, deux individus ont été étudiés.

Extraction d'ADN – Les ADN ont été extraits à partir de feuilles séchées dans du gel de silice. Le protocole utilisé est celui de Doyle et Doyle modifié (1987). Les feuilles ont été broyées dans de l'azote liquide. L'ADN total a été extrait en utilisant le tampon de lyse (TrisHCl 100mM, MAT-AB 2%, EDTA 20mM, sulfite de sodium 0,4%, PEG 1% et NaCl 1,4M) chauffé à 64°C pendant 2 heures. L'échantillon a été purifié avec le CIAA (24:1) frais. Après centrifugation à 6000rpm pendant 15 min, le surnageant a été prélevé et précipité dans un volume équivalent d'isopropanol et de 1/10^{ème} de volume d'acétate de sodium 20M. Après une in-

cubation à 20°C pendant 20 min, le mélange a été centrifugé à 6000rpm pendant 15 min pour précipiter le culot. L'ADN, sous forme de culot, a été lavé avec l'éthanol 76% puis centrifugé à 6000rpm pendant 2mn. Le culot d'ADN a été séché à température ambiante pendant 30 min. L'ADN a été ensuite re-suspendu dans 200 µl d'eau distillée et placé pendant 30 min à température ambiante. Enfin l'extrait d'ADN a été placé à + 4°C pendant une nuit.

Amplification d'ADN – La technique PCR a été répétée trois fois en utilisant trois couples d'amorces différents du génome chloroplastique: CD (trnC-trnD), HK (trnH-trnK), et SR (trnS-trnR). La réaction d'amplification d'ADN a été catalysée par une enzyme thermostable (5u/µl) en présence de désoxyribonucléotides triphosphate (20mM), du tampon d'extraction (10 ×) et de dichlorure de magnésium (m) et du Bovine Sérum Albumine (mg/ml).

Analyse RFLP – Les amplifiats ont été digérés respectivement par deux enzymes de restriction: Taq I (isolé du *Thermus aquaticus*) et Hinf I (*Haemophilus influenza*). Les fragments de restriction ont ensuite été séparés en fonction de leur taille par électrophorèse verticale sur un gel d'acrylamide 8%. Le marqueur de taille Smart Ladder SF 1Kb a été déposé de part et d'autre du gel afin de disposer une référence de taille des fragments obtenus.

Quatre systèmes amorce-enzyme de restriction ont été utilisés dans cette étude: trnC-D-Taq I, trnH-K-Taq I, trnH-K-Hinf I, et trnS-R-Hinf I.

RESULTATS

Etudes ethnobotaniques

Les différentes formes d'ignames cultivées – Toutes les ignames cultivées sont appelées *ovy* par les paysans. Pour les différencier ils ajoutent au terme *ovy* un qualificatif relatif aux caractéristiques du tubercule (couleur de la chair, forme ou taille du tubercule). Cinq formes d'ignames cultivées ont été recensées, quatre à Ankarafantsika (*ovibe*, *ovy fantaka*, *ovy voay* et *ovy lava*) et une dans la région du Menabe (*ovy toko* appelé aussi *bemako* ou *bodoa*):

- ***ovibe***: les paysans l'identifient par son tubercule pourvu de bosses et sa tête qui affleure à la surface du sol. *Ovibe* (littéralement: igname de grande taille) est doté d'un tubercule de forme arrondie et de grande taille, d'où son nom :

- ***ovy fantaka*** (ou *ovy mena*): *fantaka* est un adjectif désignant toute chose qui est enfoncée. A la différence de *ovibe*, le tubercule est plus mince, allongé et enfoui profondément dans le sol. La surface du tubercule est plutôt régulière mais ne présente pas de bosses. Le tubercule est à chair jaune rougeâtre, d'où il tire son nom *ovy mena* (igname rouge);

- ***ovy voay***: est reconnu par son tubercule de grande taille, pourvu de bosses. L'aspect général du tubercule évoque celui du crocodile (ou *voay*). La tête du tubercule sort également du sol à l'image de la tête du crocodile qui sort de l'eau :

- ***ovy lava*** (ou *ovy fotsy*): *lava* fait référence au tubercule qui est allongé. Les paysans l'ont aussi appelé *ovy fotsy* (igname blanche) à cause de la couleur de sa chair.

- ***ovy toko***: c'est la forme d'igname cultivée rencontrée à Morondava. Elle est appelée *ovy toko* (ou igname en tas) car les tubercules se vendent à l'étalage par tas et non au poids comme c'est le cas pour d'autres tubercules comme le manioc. Dans la région de Menabe, on parle aussi de *bodoa* ou de *bemako* qui veut dire "qui fait beaucoup déféquer", mais il s'agirait d'appellations secondaires qui ont été données plus récemment à l'*ovy toko*.

Système de culture d'igname – La culture d'igname se fait toujours de façon traditionnelle. D'abord, le semenceau (tête du tubercule ou bulbille) est déposé dans un trou rempli d'éléments fertilisants. Au moment de la récolte les paysans se contentent de prélever la partie consommable du tubercule et de laisser la tête dans le trou qui est immédiatement rebouché pour servir de semence l'année suivante.

Les ignames poussent dans presque tous les types de milieu, quelles que soient les conditions écologiques. La culture d'ignames ne se fait pas suivant un aménagement spécifique ni dans des champs particuliers mais les paysans les font pousser par multiplication végétative avec d'autres espèces cultivées par système de végéculture (appendice électronique: fig. 2) auprès des habitations dans les jardins de case (appendice électronique: fig. 3) ou dans les défriches. Dans ces systèmes de culture, la repousse est assurée par la replantation de la tête du tubercule après sa récolte. Elles sont également cultivées dans des lieux très éloignés du village: dans les jachères (ou *monka ala*) et dans les *baiboho* (sols alluvionnaires).

Utilisations – L'igname peut se prêter à différentes préparations culinaires. Elle est appréciée à cause de son bon goût, de sa digestibilité plus grande que celle du manioc et de son caractère plus rassasiant. Les tubercules sont consommés comme collation ou à la place du riz. Les bulbilles se préparent de la même façon que les tubercules. Les enfants s'amuse à les griller, avec ou sans la peau, comme des arachides. Les jeunes feuilles *d'ovibe* et *d'ovy fantaka* peuvent être consommées et se préparent comme des brèdes. A notre connaissance, c'est la première fois qu'il est rapporté que les feuilles d'ignames peuvent être consommées.

Les ignames cultivées sont utilisées également dans la pharmacopée traditionnelle. Les broyats des feuilles fraîches de toutes les formes de *D. alata* servent à soigner les brûlures ou les furoncles. La décoction des feuilles sèches de *ovibe*, *ovy fantaka* et *ovy toko* est utilisée pour traiter la fièvre et le paludisme. Chez les femmes et les jeunes filles, les feuilles *d'ovibe* et *d'ovy fantaka* entrent dans la préparation d'un remède contre les règles trop abondantes. Enfin, la décoction des feuilles sèches *d'ovy toko* est administrée chez les enfants atteints de rougeole.

Description botanique

Ovibe – Tige portant quatre ailes ondulées. Feuilles cordiformes arrondies (appendice électronique: fig. 4A) mesurant 17,8 cm (15,8–20,9 cm) de long et 9,8 cm (7,5–13,1 cm) de large, à pétiole ailé de 11,33 cm (10,2–13 cm) de long. Bulbilles de forme arrondie (appendice électronique: fig. 4C). Inflorescence femelle en épi composé de treize à seize fleurs à disposition spiralée le long du rachis de couleur pourpre. Fleurs femelles vues uniquement en bouton lors de nos ob-

servations. Inflorescence mâle non observée. Tubercules, généralement de grande taille, de forme irrégulière, ramifiée, cylindrique, effilée ou oblongue et dont la partie proximale renflée sort à la surface du sol (appendice électronique: fig. 4G). Tubercule solitaire ou au nombre de deux ou trois sur un même pied. Couleur de la chair jaunâtre. Poids moyen du tubercule 2 kg (0,4–4,3 kg) avec une longueur moyenne de 35,8 cm (25,5–45 cm) et un diamètre moyen de 7,8 cm (3–13 cm).

Ovy fantaka (ovy mena) – Tige anguleuse à quatre ailes continues ou ondulées de couleur violacée ou verte. Feuille cordiforme plus ou moins allongée de longueur moyenne 14,3 cm (12,8–17,5 cm), de largeur moyenne 8,9 cm (7,8–11 cm) et munie d'un pétiole ailé de 10,9 cm (10,6–11,1 cm). Non observé en fleur. Bulbilles de forme arrondie ou conique (appendice électronique: fig. 4D) et tubercule effilé ou oblong. Tubercule unique ou multiple (2 à 5) (appendice électronique: fig. 4H), de poids moyen 2,83 kg (1,2–3,3 kg), de longueur moyenne 42,33 cm (40–43 cm) et de diamètre moyen 12,33 cm (8–16 cm). Tubercule pouvant exceptionnellement atteindre 13 kg. Partie proximale du tubercule pourvue de bosses et sortant à la surface du sol. Couleur de la chair jaunâtre.

Ovy voay – Tige anguleuse, à trois et à quatre ailes violacées et ondulées. Feuilles de forme cordée arrondie ou plus allongée mesurant, en moyenne, 15,85 cm (11,4–19,45 cm) de long et 14,31 cm (11,4–14,8 cm) de large. Bulbilles de forme arrondie. Inflorescence femelle en épi composée de 18 à 28 fleurs à disposition spiralée le long du rachis de 30 à 35 cm de long. Chaque fleur est axillée par une préfeuille jaunâtre de 3 mm, à acumen pourpre très remarquable et accompagnée d'une minuscule bractée. Péricarpe, plus ou moins coriace, composé de trois sépales incurvés (2 mm) et de couleur jaunâtre, suivis de trois pétales membraneux également incurvés et jaunâtres mais de taille réduite par rapport aux sépales. Trois styles soudés à la base en un seul style trilobé dont les trois stigmates (ou lobes) sont bifides. Deux cycles d'étamines stériles (staminodes) de très petite taille (0,5 mm). Ovaire infère de couleur vert sombre et anthocyanée, d'une taille moyenne de 1,2 cm, trigone, allongé et triloculaire à deux ovules axillaires. Inflorescences mâles non observées. Fruit en capsule à trois valves, deux graines ailées et albuminées (1 mm). Tubercule effilé, oblong ou fusiforme, présentant sur la moitié supérieure des bosses (appendice électronique: fig. 4E). Tubercule généralement solitaire dont la tête apparaît au ras du sol. Couleur de la chair jaunâtre. Poids moyen du tubercule 4,15 kg (3,3–5,8 kg) avec une longueur moyenne de 48,8 cm (47–49 cm) et un diamètre moyen de 13 cm (11–15 cm).

Ovy lava (ovy fotsy) – Tige anguleuse à trois puis quatre ailes ondulées et violacées. Feuille cordiforme arrondie mesurant en moyenne 16,95 cm de long (10,3–23,2 cm) et 9,98 cm de large (8–11,8 cm) et à pétiole ailé de longueur moyenne 10 cm (9–11 cm). Non vue en fleur. Bulbilles de forme arrondie. Tubercule plus mince et unique, de différentes formes: effilée, oblongue ou fusiforme (appendice électronique: fig. 4F). Corne enfouie ou dépassant du sol. Poids moyen du tubercule 1,48 kg (0,5–3,6 kg) et de dimensions moyennes 38,75 cm de long (22–57 cm) et 7,5 cm de large (5–10 cm). Chair du tubercule de couleur blanche.

Ovy toko (bemako ou bodoa) – Tige anguleuse à trois ou à quatre ailes de couleur verte ou violacée. A la base de la tige de certains individus, les ailes sont transformées en épines (appendice électronique: fig. 4B). Feuille cordée allongée ou arrondie de dimensions moyennes 17,2 cm (11,4–19,9 cm) de long et 9,3 cm (7,9–12,8 cm) de large, à pétiole ailé de longueur moyenne 10,2 cm (9,5–12,8 cm). Absence ou présence de fleurs femelles, suivant les pieds. Inflorescences femelles, à l'aisselle des feuilles, composées d'un ou deux épis de longueur moyenne 30 cm dont chaque épi comporte environ quatorze à vingt fleurs alternes à disposition alternée spiralée le long du rachis de couleur pourpre, à section ovale et plus ou moins tordu. Ovaire, infère, trigone, allongé, de taille moyenne 1,5 cm et triloculaire à deux ovules axillaires. Fleur de taille moyenne 5 mm composé de trois sépales (3 mm), de trois pétales (2 mm) de couleur jaunâtre et de trois styles (0,6 mm). Inflorescence mâle non observée. Bulbilles de formes ovoïde, conique ou arrondie suivant les pieds. Tubercule unique ou double, à chair jaunâtre, généralement cylindrique, oblong ou effilé. Tête du tubercule enfouie ou sortant du sol. Poids moyen du tubercule 2,2 kg (0,8–4,25 kg), de longueur moyenne 36,3 cm (20–52 cm) et de diamètre moyen 7,7 cm (3,6–12 cm). Tubercule atteignant 15 kg dans certains cas.

Etudes morphométriques

Les traitements statistiques font ressortir qu'à la différence des quatre autres formes, *ovy voay* se distingue par des valeurs moyennes significativement élevées sauf pour la longueur de l'acumen dont la valeur moyenne est la plus basse (tableau 1).

Après l'application du test de Newman-Keuls, l'existence de deux groupes de *D. alata* a été révélée: un groupe statistiquement homogène rassemblant *ovibe*, *ovy fantaka*, *ovy lava* et *ovy toko* et un second groupe incluant seulement *ovy voay*.

Etudes moléculaires

Avec les quatre combinaisons amorce-enzyme de restriction (trnCD-Taq I, trnHK-Taq I, trnHK-Hinf I, et trnSR-Hinf I), aucune diversité génétique ne différencie les cinq formes de *D. alata*. La combinaison trnCD-Taq I (appendice électronique: fig. 5) montrent que toutes les formes de *D. alata* (*ovibe*, *ovy fantaka*, *ovy voay*, *ovy lava* et *ovy toko*) présentent chacune le même profil de restriction, différent de celui de l'espèce *D. maciba* (espèce utilisée comme référence). La digestion enzymatique de chaque fragment amplifié a généré cinq fragments de différentes longueurs, mettant ainsi en évidence quatre sites de restriction chez les échantillons de *D. alata* et quatre bandes avec trois sites de restriction chez *D. maciba*. Les cinq formes de *D. alata* possèdent, à la fois, les mêmes fragments de restriction à 1200pb, à 620pb, à 160pb, à 100pb et à 50pb tandis que *D. maciba* possède quatre fragments à 900pb, à 700pb, à 620pb et à 100pb dont les deux premières bandes sont spécifiques. A ce stade d'analyse, les cinq formes de *D. alata* provenant d'Ankarafantsika, de Morondava et de Mahabo apparaissent appartenir à un même cultivar.

Tableau 1 Différence entre les cinq formes d'ignames cultivées par analyse de variance (ANOVA).

Pour chaque colonne, les moyennes suivies d'une (ou des) mêmes lettres ne sont pas significativement différentes et constituent un groupe statistiquement homogène, selon le test de Newman-Keuls ($p = 0,05$).

LONG EN, longueur de l'entre-nœud; DIAM EN, Diamètre de l'entre-nœud; LONG PET, longueur du pétiole; LARG SIN, largeur du sinus; LARG AUR, largeur de l'auricule; LONG AUR, longueur de l'auricule; LARG LIM, largeur du limbe; LONG LIM, longueur du limbe; LONG ACUM, longueur de l'acumen; LONG TUB, longueur du tubercule; DIAM TUB, diamètre du tubercule; POIDS TUB, poids du tubercule; NS, non significatif; HS, hautement significatif.

	LONG EN (cm)	DIAM EN (cm)	LONG PET (cm)	LARG SIN (cm)	LARG AUR (cm)	LONG AUR (cm)	LARG LIM (cm)	LONG LIM (cm)	LONG ACUM (cm)	LONG TUB (cm)	DIAM TUB (cm)	POIDS TUB (kg)
<i>Ovibe</i>	17,43a	0,30ab	11,40a	1,08b	4,80a	3,30b	9,95b	17,05a	2,01a	37,00b	10,16ab	2,46bc
<i>Ovy fantaka</i>	16,60a	0,26b	10,93a	0,76b	4,70a	3,31b	8,95b	14,28a	1,56bc	42,33b	12,33a	2,83b
<i>Ovy lava</i>	17,22a	0,25b	10,00a	1,17b	5,57a	4,45a	9,98b	16,95a	1,81ab	38,75b	7,50b	1,48c
<i>Ovivoay</i>	19,26a	0,36a	10,66a	1,58a	5,13a	4,86a	13,08a	15,85a	1,50c	48,00a	13,00a	4,15a
<i>Ovy toko</i>	16,17a	0,32ab	9,94a	0,90b	4,90a	3,66b	9,06b	16,90a	1,70bc	41,07b	8,79ab	2,34bc
Probabilité théorique	0,05	0,05	0,05	0,05	0,05	0,05	0,05	0,05	0,05	0,05	0,05	0,05
Probabilité calculée	0,2240	0,0042	0,3947	0,0014	0,1648	0,0006	0,0000	0,1509	0,0006	0,0015	0,0006	0,0001
Significativité	NS	HS	NS	HS	NS	HS	HS	NS	HS	HS	HS	HS

DISCUSSION

Avant le 18^{ème} siècle, les ignames ont été cultivées dans de véritables champs qui leur étaient dédiés (Perrier de la Bâthie 1925) mais, actuellement, les ignames ne sont plus plantées que sous forme de quelques pieds dans les cours des habitations ou mélangées à d'autres cultures dans les champs (végéculture). Le mode de culture de l'igname diffère des systèmes monocultureux pratiqués dans les pays producteurs et consommateurs d'igname. C'est ce qui se passe notamment en Afrique où la culture de l'igname se fait au niveau de champs très élaborés avec des buttes ou des billons. A Madagascar, la culture de l'igname se fait actuellement de manière extensive, sans labour ni entretien particulier porté aux plants d'ignames. Seul le *dina* (ou pacte social assorti de sanctions) qui existe chez le Betsimisaraka et qui stipule que chaque tête d'igname déterrée doit être replantée (Jeannoda et al. 2003) témoigne de l'importance attribuée jadis à la culture de l'igname.

La consommation des feuilles d'igname à Ankarafantsika semble être une 'originalité de Madagascar. A notre connaissance aucune autre consommation de feuilles n'a encore été rapportée dans le reste du Monde.

Une variabilité morphologique a été observée chez les cinq formes de *D. alata*. Elle affecte essentiellement la forme des tubercules, des feuilles et des bulbilles. Degras (1986) a constaté que *D. alata* est une espèce à morphotypes très divers et difficiles à séparer. Par ailleurs, la diversité morphologique des tubercules chez cette espèce a déjà été soulignée dans les littératures les plus anciennes, entre autres, Bourret (1973) ou Prain & Burkill (1939) qui ont trouvé 71 formes de tubercules. Cette variation pourrait résulter d'une interaction avec les types de sols ou techniques de culture. Ainsi les différentes formes de *D. alata* observées pourraient être seulement des écotypes dont la morphologie est le résultat des conditions du milieu.

Des études morphométriques des ignames ont été déjà menées dans d'autres pays. En Nouvelle Calédonie, Bourret (1973) a travaillé sur cent formes de *D. alata* en utilisant vingt caractères (incluant la longueur et la vigueur de la plante, la longueur et la forme des feuilles, les caractéristiques de la tige et des ailes, la présence et l'absence de bulbilles ainsi que la forme et la couleur des tubercules). Ainsi, les formes pouvaient être regroupées selon quatre catégories majeures de morphotypes. De même, Martin & Rhodes (1977) ont classé 235 formes de *D. alata* en utilisant 28 descripteurs morphologiques et ont trouvé jusqu'à quinze groupes principaux constituant les principales branches d'un arbre phylogénétique. Ils ont également montré que les cultivars de *D. alata* sont classés en des groupes qui peuvent varier suivant leurs origines géographiques ou suivant l'intervention de l'homme.

En appliquant la technique RFLP-PCR avec quatre systèmes amorce-enzyme de restriction qui concerne le génome chloroplastique, aucune diversité génétique n'a pu être mise en évidence au sein de *D. alata* à l'ouest de Madagascar. Au stade actuel de nos recherches, les cinq formes de *D. alata* appartiendraient donc à un seul et même cultivar.

Cependant, notre étude moléculaire ne s'est focalisée que sur trois régions génomiques de l'ADN chloroplastique, ce qui est encore loin d'être représentatif pour l'ensemble du génome de la plante. Aussi, devrions-nous poursuivre les recherches et recourir à l'application d'autres systèmes amorce-enzyme de restriction ou à l'utilisation d'autres méthodes de marquages moléculaires tels que les microsatellites ou l'AFLP (Amplified Fragment Length Polymorphism). A cet égard, les études moléculaires dans d'autres régions du monde ont montré l'existence de différents cultivars au sein de l'espèce *D. alata* à l'exemple de celles d'Egesi et al. (2006) en Afrique et de Malapa (2000) au Vanuatu.

CONCLUSION ET PERSPECTIVES

Les cinq formes inventoriées de *D. alata* se distinguent par la morphologie de leurs tiges, feuilles, tubercules, bulbilles et par la présence ou l'absence de fleurs. Une étude morphométrique basée sur des analyses statistiques (tests ANOVA et de Newman-Keuls) ont permis de mettre en évidence l'existence de deux groupes distincts de *D. alata*. Cependant, les études moléculaires avec l'utilisation de quatre systèmes amorce-enzyme de restriction selon la méthode RFLP-PCR n'ont pas permis de confirmer les résultats des études morphométriques. Ainsi, l'existence de plusieurs cultivars de *D. alata* dans l'ouest de Madagascar n'est pas encore un fait avéré. Le recours à d'autres méthodes de marquage moléculaire plus polymorphes telles que les microsatellites est nécessaire pour poursuivre et affiner notre recherche. Le comptage chromosomique ainsi que la recherche du niveau de ploïdie sont également recommandés.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> > SBB50 > dossier 582) et comprend un appendice électronique au format pdf (figures relatives aux ignames cultivées de Madagascar).

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Manuscript received 31 Oct. 2010; accepted in revised version 20 Apr. 2011.

Communicating Editor: Rainer Bussmann.



Diversity and origin of medicinal exotic flora in Cape Verde Islands

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Background and aims – The Cape Verde Islands were discovered by Portuguese navigators who, throughout the 15th century, explored the African coasts. Despite the recognised value of the Cape Verde flora, the study of medicinal plants is still incipient. The main goal of the present study was to understand the ancestral uses of the exotic medicinal flora that the population of the archipelago still uses, allowing some considerations for the geographic origin of these species.

Methods – This study is mostly based on the collection of ethnobotanical data obtained in specimens housed in LISC Herbarium and in available botanical and historical bibliographic data.

Key results – A checklist of the exotic medicinal plants of Cape Verde is presented. The use of local flora in folk medicine is common, and 101 exotic naturalized taxa were reported as medicinal in this archipelago. Most of these plants arise from Afrotropical, Neotropical, Palaeartic, or Pantropical regions. Furthermore nineteen non-naturalized exotic taxa, mainly from Neotropical and Oriental regions, were reported as medicinal.

Conclusions – This study shows the relevance of historical factors in the determining the composition of the medicinal flora in Cape Verde, namely the importance that the slave trade routes from Africa to the Americas played during the period of the 16th–19th centuries. It also allows the recognition and positive valuation of the cultural and biological Cape Verde's patrimony and its sustainable use.

Key words – West Africa, medicinal plants, non-indigenous flora, species distribution, history of plant use, traditional medicine.

INTRODUCTION

The Cape Verde archipelago is located in the North Atlantic Ocean, in close proximity to the western African coast, c. 600 km west of Senegal. All the nine inhabited islands are of volcanic origin, namely: Santo Antão, São Vicente, São Nicolau (Northern Islands), Santiago, Fogo, Brava (Southern Islands), and Sal, Boavista and Maio (Eastern Islands) (fig. 1). This archipelago was discovered by Portuguese navigators who, throughout the 15th century, explored the African coast (Albuquerque 1991). Documents relating to its discovery do not record the existence of any traces of human occupation, but mention the existence of several plant species that attracted the attention of their first occupants (Cardoso 1902). The colonization of Cape Verde, which began around 1460 in Santiago Island, was laid by Europeans, mainly Portuguese but also some Spanish, a few Italians, and Africans purchased on the West African coast, especially on the Guinea coast (slave trade) (Ribeiro 1955). The geographical position of Cape Verde in the Atlantic Ocean transformed these islands into an important port of call for the supply and repair of the Portuguese vessels (Carreira 1986). In the main port city of

Santiago Island, Ribeira Grande, sailors from Portugal, traders on their way to Central America or Brazil, and travellers returning from the East, exchanged experiences and knowledge and left some plants brought from distant locations that served to prevent and cure most illnesses (Torrão & Soares 2009).

Although the introduction of many plants in Cape Verde seems to have been intentional, the availability of old descriptions of the plant uses in these islands is scarce (Duarte & Moreira 2002). In general, the lack of registered thorough sampling until the middle of the 19th century was a result of the fact that botanists visiting this archipelago were only taking advantage of their short stops on the way to more botanically rich regions for collection and study of the local flora (Pettersson 1960). In fact, it was only in the 19th century that these islands began to raise the interest among the naturalists and scientists, and some field expeditions were made by Forbes in 1822, Darwin in 1832, Hooker in 1839, Bolle in 1851, and Welwitsch in 1853 and 1861 (Barbosa 1961). In the 19th and 20th centuries several important works were published (e.g. Webb 1849, Schmidt 1852, Chevalier 1935,

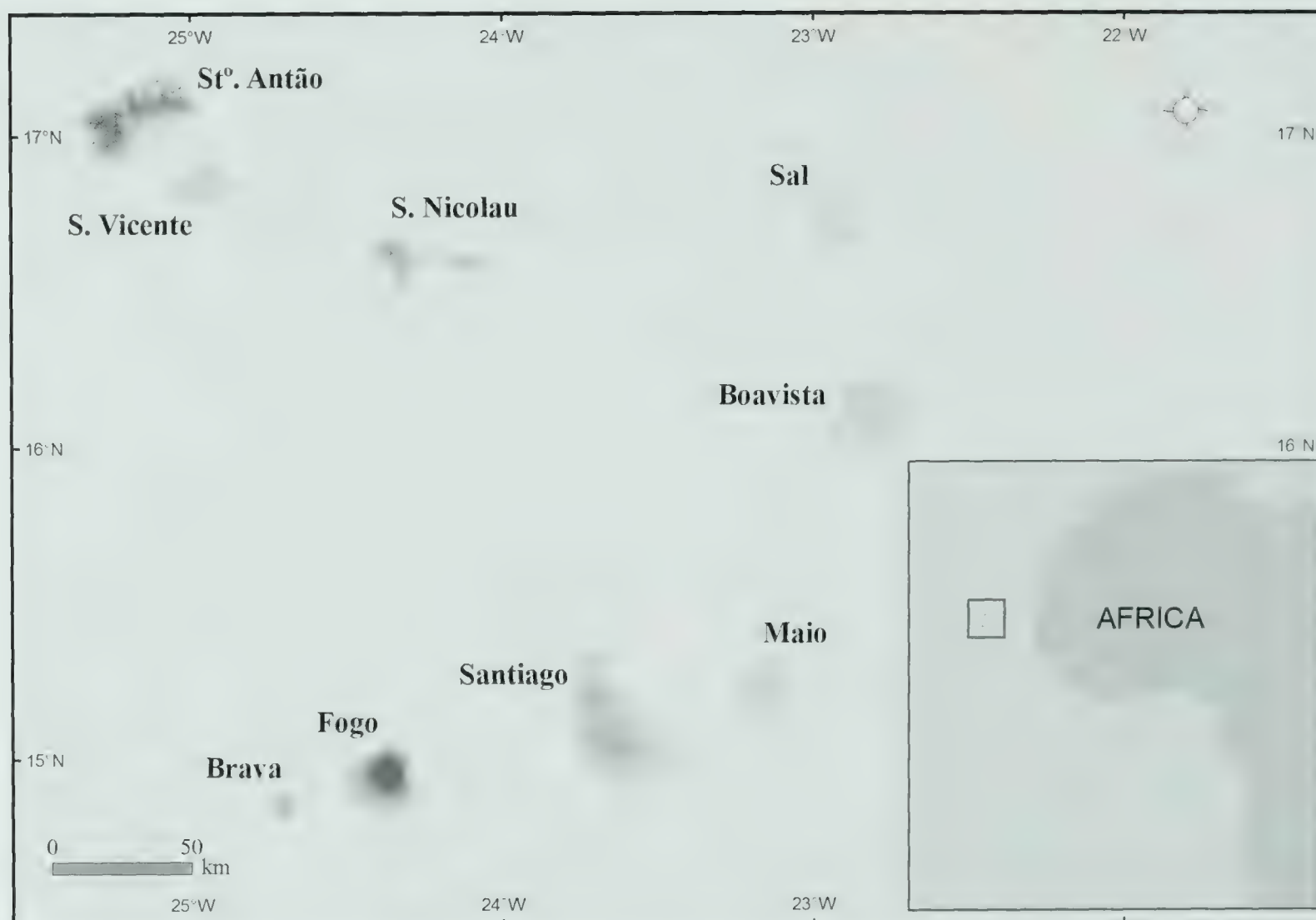


Figure 1 – Geographic location of Cape Verde archipelago in the North Atlantic Ocean.

Hansen & Sunding 1993, Brochmann et al. 1997, Paiva et al. 1995–1996, Martins et al. 2002) providing a reasonable insight into the knowledge of the Cape Verde flora. Despite these and other botanical studies, several important issues remain to be considered, namely related to the collection of ethnobotanical data. The few studies available concerning the uses of medicinal plants in this archipelago (namely Barbosa 1961, Gomes et al. 1995, Varela 1999, 2001, and Vera-Cruz 1999) are written in Portuguese, which increases the difficulty for the scientific community to access the information.

Despite the subtropical dry climate that characterizes this archipelago, and which has not allowed the development of abundant vegetation, the Cape Verde flora comprises about 740 spontaneous or naturalized taxa from more than one hundred families, the Asteraceae, Euphorbiaceae, Fabaceae, Malvaceae, Solanaceae, Cyperaceae, and Poaceae being the most well-represented (Duarte et al. 2008). Most of the archipelago's flora is presently composed of exotic naturalized species (Duarte & Romeiras 2009).

Since the Cape Verde Islands were not inhabited up to the end of the 15th century (Cardoso 1902), it will be helpful to understand how the introduction of plants for medicinal purposes, constituted a factor in defining the present day flora. As such, herein is presented a study that has been developing in the field of characterization of the Cape Verde exotic medicinal flora, in order to understand the traditional use of the exotic medicinal flora that the population of this archipelago still uses and to highlight some features related to their introduction during islands colonization.

MATERIAL AND METHODS

Data was gathered from published research papers on medicinal plant studies in Cape Verde (Barbosa 1961, Gomes et al. 1995, Vera-Cruz 1999, Varela 1999, 2001) and complemented by exhaustive consultation of specimens kept in LISC Herbarium (IICT/Tropical Research Institute), which holds the most important collection of Cape Verde flora. For each taxon, the family, scientific and local name, habit and distribution in Cape Verde (only inhabited islands) and worldwide native range were included in a database. This data was gathered in Chevalier (1935), Brochmann & Rustan (1981), *Flora de Cabo Verde* (Paiva et al. 1995–1996, Martins et al. 2002), *Flore du Sénégal* (Berhaut 1971, 1974, 1975a, 1975b, 1976, 1979, Vanden Berghen 1988, 1991), *Flora of West Tropical Africa* (Hepper 1963, 1968–1972, Hutchinson & Dalziel 1954–1958), Hansen & Sunding (1993), and Sánchez-Pinto et al. (2005) as well as in several published papers related with particular taxa. Also data collected in recent field work done by the authors was taken into consideration. Data concerning the origin (native vs. introduced) of the species was mainly obtained from Lobin & Zizka (1987), Ferrão (1993) and Sánchez-Pinto et al. (2005). However with some taxa it was not possible to obtain accurate data since their geographic origin is unknown or doubtful.

The scientific names were revised and updated using on-line databases such as Tropicos (<http://www.tropicos.org>).

For the exotic plants used in traditional medicine in Cape Verde, the data was organized in two categories: (a) the naturalized species, i.e. the introduced plants that have shown the

Table 1 – Checklist of the exotic naturalized medicinal plants of Cape Verde Islands.

(a), the taxa in which the introduced status in Cape Verde is somewhat doubtful are marked with an asterisk (*), (b), in the case of recent nomenclatural changes, synonyms commonly employed in Cape Verdean botanical literature are included; (c), the terminology used follows Morrone (2002). Whenever possible, the distribution of each taxon concerns to its native geographic range; (d), Cape Verde Islands abbreviations: A, Santo Antão; V, São Vicente; N, São Nicolau; S, Sal; B, Boavista; M, Maio; T, Santiago; F, Fogo; and Br, Brava.

family scientific name ^{(a) (b)}	local name	native distribution ^(c)	habit	distribution in Cape Verde ^(d)
DICOTYLEDONEAE				
Amaranthaceae				
<i>Achyranthes aspera</i> L. var. <i>sicula</i> L.	malpica	Afrotropical	perennial herb	A, V, N, M, T, F, Br
* <i>Aerva javanica</i> (Burm.f.) Juss.		Afrotropical	perennial herb	A, V, N, S, B, M, T, F, Br
<i>Alternanthera sessilis</i> (L.) R.Br. ex DC.	mo-na-pé	Afrotropical	annual or perennial herb	A, V, T
<i>Amaranthus hybridus</i> L. subsp. <i>hybridus</i>	breto-macho	Oriental	annual herb	A, T
<i>Amaranthus spinosus</i> L.	breto-espinhoso	Neotropical	annual herb	A, V, N, B, M, T, F, Br
<i>Amaranthus viridis</i> L.	breto	Afrotropical	annual herb	V, T
<i>Celosia trigyna</i> L.		Afrotropical	annual herb	A, T
<i>Gomphrena globosa</i> L.		Oriental	annual herb	N, T
Apiaceae				
<i>Anethum graveolens</i> L.	endre, ente, endro, erva-doce	Palaeartic	annual herb	N, B, T, F, Br
<i>Foeniculum vulgare</i> Mill.	erva doce, funcho	Palaeartic	perennial herb	A, V, N, T, F, Br
Apocynaceae				
<i>Nerium oleander</i> L.	loendro, cevadinha	Palaeartic	shrub	A, V, N, S, B, M, T, F
Asclepiadaceae				
* <i>Calotropis procera</i> (Aiton) W.T.Aiton	bombardeiro	Afrotropical- Oriental	shrub	A, V, N, S, B, M, T, F, Br
Asteraceae				
<i>Acanthospermum hispidum</i> DC.	carrapiça, espinho-de- cigano	Neotropical	annual herb	A, V, N, S, M, T, F, Br
<i>Ageratum conyzoides</i> L.	oregão, matinho-de- lisboa	Pantropical	annual herb	A, V, N, S, T, F, Br
<i>Blainvillea gayana</i> Cass.		Afrotropical	annual herb	A, V, N, M, T, F, Br
<i>Centaurea melitensis</i> L.	unha-de-gato-bastarda	Palaeartic	annual or biennial herb	A, N, T, Br
<i>Cichorium intybus</i> L.	chicoria	Palaeartic	perennial herb	A
* <i>Crassocephalum rubens</i> (Juss. ex Jacq.) S.Moore		Afrotropical	annual herb	N, F, Br
<i>Eclipta prostrata</i> (L.) L. (= <i>Eclipta alba</i> (L.) Hassk.)		Afrotropical- Neotropical	annual herb	T, Br
<i>Sclerocarpus africanus</i> Jacq. ex Murray		Afrotropical- Oriental	annual herb	M, T, F
<i>Sonchus oleraceus</i> L.	serralha, algodão-de- garça	Palaeartic	annual or biennial herb	A, V, N, S, M, T, F, Br
<i>Synedrella nodiflora</i> (L.) Gaertn.		Neotropical	annual herb	A, N, T, F, Br
<i>Vernonia cinerea</i> (L.) Less.		Afrotropical	annual or biennial herb	A, V, N, I, F
<i>Vernonia colorata</i> (Willd.) Drake		Afrotropical	shrub	N, F
Boraginaceae				
* <i>Heliotropium crispum</i> Desf.	alfavaca, três marias, furtaragem	Afrotropical- Palaeartic	perennial herb	A, V, N, S, B, M, T, F, Br

Table 1 (continued) – Checklist of the exotic naturalized medicinal plants of Cape Verde Islands.

family scientific name ^{(a) (b)}	local name	native distribution ^(c)	habit	distribution in Cape Verde ^(d)
DICOTYLEDONEAE				
Boraginaceae				
<i>*Heliotropium pterocarpum</i> (DC. & A.DC.) Hochst. & Steud. ex Bunge.	alfavaca, mama-bitcho	Afrotropical	perennial herb	A, V, N, B, M, T
Brassicaceae				
<i>Brassica nigra</i> (L.) W.D.J.Koch	mostarda-preta	Palaeartic	annual herb	A, V, N, T, Br
<i>Nasturtium officinale</i> R.Br.	agrião	Cosmopolitan	perennial herb	A, V, N, T, F, Br
Cactaceae				
<i>Opuntia ficus-indica</i> (L.) Mill.	tabaibo, figueira-do-inferno	Neotropical	shrub	A, N, T, F
Chenopodiaceae				
<i>Chenopodium ambrosioides</i> L.	fedegosa, cha-de-ribeira, palha-teixeira	Neotropical	annual herb	A, V, N, B, M, T, F, Br
<i>Chenopodium murale</i> L.	fedegosa, padja gosa	Palaeartic	annual herb	A, V, N, S, B, M, T, F, Br
Convolvulaceae				
<i>Ipomoea muricata</i> (L.) Jacq. (= <i>Ipomoea turbinata</i> Lag.)	calabaceira	Neotropical	annual or perennial herb	A, N, M, T, F
Cucurbitaceae				
<i>Momordica charantia</i> L.	banana-rato, sacaitano, aboborinha são caetano	Pantropical	perennial herb	A, V, N, B, M, T, F, Br
Euphorbiaceae				
<i>Jatropha curcas</i> L.	purga, purgueira	Neotropical	shrub or small tree	A, V, N, S, B, M, T, F, Br
<i>Ricinus communis</i> L.	bafareira, djaqui, ricino	Afrotropical	annual or perennial herb	A, V, N, M, T, F, Br
Lamiaceae				
<i>*Ajuga iva</i> (L.) Schreb. var. <i>pseudoiva</i> (Labill. & Castagne ex DC.) Steud.	piorrinho, mata-piolho	Palaeartic	perennial herb	A, V, N, S, T
<i>*Lavandula coronopifolia</i> Poir. var. <i>coronopifolia</i>	risco	Afrotropical-Palaeartic	perennial herb	A, V, N, S, T, Br
<i>*Lavandula dentata</i> L.	rosmaninho	Palaeartic	shrub	A, F, Br
<i>Leucas martinicensis</i> (Jacq.) R.Br.	morroio	Afrotropical	annual herb	A, V, N, M, T, F, Br
<i>Ocimum basilicum</i> L.	magericão	Palaeartic	perennial herb	A, N, T, F
<i>Rosmarinus officinalis</i> L.	alecrim	Palaeartic	shrub	A, F
Leguminosae (s. lat.)				
Caesalpiniaceae				
<i>*Chamaecrista absus</i> (L.) H.S.Irwin & Barneby		Afrotropical-Oriental	annual herb	A
<i>*Chamaecrista nigricans</i> (Vahl) Greene (= <i>Cassia nigricans</i> Vahl)	tintêro	Afrotropical-Oriental	annual herb	N, F
<i>*Senna italica</i> Mill. (= <i>Cassia italica</i> (Mill.) Lam. ex F.W.Andrews)	cêni, senna, seno	Afrotropical	perennial herb	A, V, N, S, B, M, T, F
<i>Senna occidentalis</i> (L.) Link	baginha, pintchera	Neotropical	annual or perennial herb	A, V, N, S, B, M, T, F, Br
<i>Tamarindus indica</i> L.	tamarindo, tambarina	Afrotropical-Oriental	tree	A, V, N, S, M, T, F, Br

Table 1 (continued) – Checklist of the exotic naturalized medicinal plants of Cape Verde Islands.

family scientific name ^{(a) (b)}	local name	native distribution ^(c)	habit	distribution in Cape Verde ^(d)
DICOTYLEDONEAE				
Fabaceae				
<i>*Abrus precatorius</i> subsp. <i>africanus</i> Verdc.	santa-clara	Pantropical	perennial herb	A, N, T, F, Br
<i>Cajanus cajan</i> (L.) Huth	feijão-congo	Oriental	shrub	A, N, B, T, F, Br
<i>Clitoria ternatea</i> L.	palha-lobes, bacinha-de-codorniz	Pantropical	perennial herb	A, N, B, M, T, Br
<i>Crotalaria retusa</i> L. var. <i>retusa</i>	beijinho, flor-de-lagartixa	Pantropical	perennial herb	A, N, B, T, F, Br
<i>Desmodium hirtum</i> Guill. & Perr.	maratchinga, marquinha	Afrotropical	perennial herb	A, M, F
<i>Indigofera hirsuta</i> L. var. <i>hirsuta</i>	banana-santcho	Afrotropical	annual herb	N, T, F
<i>Indigofera tinctoria</i> L.	tinta, tinteiro	Oriental	shrub	A, N, B, M, T, F, Br
<i>Lonchocarpus laxiflorus</i> Guill. & Perr.		Afrotropical	small tree	A, T
<i>Mucuna pruriens</i> (L.) DC.	nganhoma	Afrotropical-Oriental	annual herb	A, T
<i>Rhynchosia minima</i> (L.) DC.	feijoeiro-de-lagartixa	Pantropical	perennial herb	A, V, N, S, B, M, T, F, Br
<i>Sesbania grandiflora</i> (L.) Pers.	monduro	Oriental	shrub	T, F
<i>Stylosanthes fruticosa</i> (Retz.) Alston		Afrotropical	perennial herb	T, F
<i>Tephrosia purpurea</i> (L.) Pers. subsp. <i>leptostachya</i> (DC.) Brummitt		Afrotropical-Oriental	perennial herb	V, B, T, F
<i>Zornia glochidiata</i> Rchb. ex DC.		Afrotropical	annual herb	A, V, N, M, T, F
Mimosaceae				
<i>Leucaena leucocephala</i> (Lam.) de Wit	acacia, linhacho, leucena	Neotropical	shrub or small tree	A, V, N, S, B, T, F, Br
Malvaceae				
<i>*Abutilon pannosum</i> (G.Forst.) Schltdl.	lolo-branco, malva	Afrotropical-Oriental	perennial herb	A, V, N, S, B, M, T, F, Br
<i>Gossypium barbadense</i> L.		Neotropical	shrub	A, N, T, F
<i>Gossypium hirsutum</i> L.	algodoeiro	Neotropical	subshrub	A, V, N, B, M, T, F, Br
<i>Hibiscus cannabinus</i> L.		Afrotropical-Oriental	annual herb	M, T
<i>Hibiscus surattensis</i> L.		Afrotropical-Oriental	perennial herb	F
<i>Lavatera cretica</i> L.	malva	Palaeartic	annual herb	A, V, T
<i>Malva parviflora</i> L.	malvinha, marbinha	Palaeartic	annual herb	A, V, N, B, M, T, F, Br
<i>*Sida acuta</i> Burm. f.	lolô	Pantropical	annual herb	A, N, B, M, T, F, Br
<i>*Sida alba</i> L.	lôlô-fino	Pantropical	perennial herb	A, V, N, S, B, M, T
<i>*Sida cordifolia</i> L.		Pantropical	perennial herb	A, N, B, T, F
<i>*Sida rhombifolia</i> L.	lolô, loulo-preto-grande	Pantropical	annual herb	A, V, N, M, T, F, Br
<i>Urena lobata</i> L.		Pantropical	perennial herb	I, F
Meliaceae				
<i>Melia azedarach</i> L.	intendente, tendente, viúva	Oriental-Australotropical	tree	A, V, N, S, B, T, I, Br

Table 1 (continued) – Checklist of the exotic naturalized medicinal plants of Cape Verde Islands.

family scientific name ^{(a) (b)}	local name	native distribution ^(c)	habit	distribution in Cape Verde ^(d)
DICOTYLEDONEAE				
Moringaceae				
<i>Moringa oleifera</i> Lam.	acácia-branco, moringa	Oriental	small tree	A, S, M, T, F
Papaveraceae				
<i>Argemone mexicana</i> L.	cardo, cardo-santo	Nearctic- Neotropical	annual herb	A, V, N, S, B, M, T, F, Br
Plantaginaceae				
<i>Plantago major</i> L.	fedegosa, tanchagem	Palaeartic	perennial herb	A, V, N, T, F, Br
Plumbaginaceae				
<i>Plumbago zeylanica</i> L.	fogo-da-serra, pega- cabrito	Pantropical	perennial herb	A, N, T, F, Br
Rubiaceae				
<i>Spermacoce verticillata</i> L. (= <i>Borreria verticillata</i> (L.) G.Mey.)	bedjo-teso, beio-teso	Afrotropical- Neotropical	subshrub	N, T, F, Br
<i>Mitracarpus hirtus</i> (L.) DC. (= <i>Mitracarpus scaber</i> Zucc. ex Schult. & Schult. f.)	beitece, beiteso, locotém	Pantropical	annual herb	B, F, Br
Rutaceae				
<i>Ruta chalepensis</i> L.	arruda	Palaeartic	subshrub	A, N, T
Sapindaceae				
<i>Sapindus saponaria</i> L.	sapodilha, avelera, aveloa	Nearctic- Neotropical	shrub or small tree	A, T, F
Scrophulariaceae				
<i>Capraria biflora</i> L.		Neotropical	shrub	A, N
Solanaceae				
<i>Datura inoxia</i> Mill.	barbiaca-preta, barbidjaca	Neotropical	annual or perennial herb	A, V, N, B, M, T, F, Br
<i>Datura metel</i> L.	berbilhaca-roxa, berbilhaca	Neotropical	annual or perennial herb	A, N, F
<i>Datura stramonium</i> L.	barbilhaca, ervilhaca, estramónio	Nearctic	annual or biennial herb	A, N, S, B, M, T, F, Br
<i>Nicotiana glauca</i> Graham	chaluteiro, charroteira	Neotropical	annual or perennial herb	A, V, N, S, B, M, T, F, Br
<i>Physalis lagascae</i> Roem. & Schult.	malua	Neotropical	annual herb	T
<i>Solanum nigrum</i> L. subsp. <i>nigrum</i>	malagueta-de-galinha, sta-maria	Palaeartic- Oriental	annual or perennial herb	A, V, N, B, M, T, F, Br
* <i>Withania somnifera</i> (L.) Dunal	malagueta-de-galinha, pontadeira	Afrotropical- Oriental	perennial herb	A, V, N, B, T, F, Br
Verbenaceae				
<i>Lantana camara</i> L.	freira, kambara, lantana	Neotropical	shrub	A, V, N, B, T, F, Br
<i>Verbena officinalis</i> L.	agibon-da-terra, gibon	Palaeartic	annual or perennial herb	A, T, Br
MONOCOTYLEDONEAE				
Agavaceae				
<i>Agave sisalana</i> Perrine ex Engelm.	carapate-manila	Neotropical	shrub	A, V, N, T, F, Br
<i>Furcraea foetida</i> (L.) Haw.	carapate	Neotropical	shrub	A, V, N, T, F, Br
Asphodelaceae				
<i>Aloe vera</i> (L.) Burm. f.	babosa	Palaeartic	perennial herb	A, V, N, B, M, T, F, Br

Table 1 (continued) – Checklist of the exotic naturalized medicinal plants of Cape Verde Islands.

family scientific name ^{(a) (b)}	local name	native distribution ^(c)	habit	distribution in Cape Verde ^(d)
MONOCOTYLEDONEAE				
Commelinaceae				
<i>Commelina diffusa</i> Burm. f. subsp. <i>diffusa</i>	palha-de-água	Pantropical	annual herb	A, N, T
Cyperaceae				
* <i>Cyperus amabilis</i> Vahl		Pantropical	annual herb	F
<i>Cyperus esculentus</i> L.	vista	Pantropical	perennial herb	A, N, B, T, F
<i>Cyperus rotundus</i> L.	junca, injunça	Pantropical	perennial herb	A, V, N, M, T, F
* <i>Kyllinga pumila</i> Michx.		Afrotropical- Neotropical	annual herb	T
Poaceae				
<i>Imperata cylindrica</i> (L.) Raeusch.		Afrotropical	perennial herb	F

ability to reproduce themselves, and to spread without direct human assistance (table 1); and (b) the non-naturalized species (table 2).

Based on cited bibliography we further analyzed the native distribution range of these exotic medicinal plants. The terminology used follows Morrone (2002), which considers the following world regions: Nearctic, Palaearctic, Neotropical, Afrotropical, Oriental, Australotropical, Andean, Cape or Afrotemperate, and Antarctic. Furthermore some combinations were considered for species with a more wide range of distribution: Cosmopolitan, Pantropical, Afrotropical-Neotropical, Afrotropical-Palaearctic, Afrotropical-Oriental, Oriental-Australotropical and Nearctic-Neotropical. It has to be noted that with some species, especially the widespread, it was not possible to determine the exact range of native distribution.

Moreover, an historic contextualization of the introduction of the medicinal plants in Cape Verde was also carried out using for instance the descriptions of the English Captain Georges Roberts in 1726 (in Roberts 1980), or from the naturalist Feijó in 1797, in charge of collecting information on the natural productions and responsible for the first herbarium representing the Cape Verde flora (in Feijó 1986). Other historical documents with descriptions and information referring to the colonization of these islands were used, e.g. Senna 1818 (in Senna 1987), Chelmicki & Varnhagen 1841, and Valdez 1864.

In addition to the mentioned studies and taking into consideration the fact that most of the slaves that initially populated Cape Verde came from Guinea-Bissau, we further compared the exotic medicinal flora of both countries using Catarino et al. (2008) checklist.

RESULTS

Exotic flora used in traditional medicine

A total of 101 naturalized exotic species were reported in traditional medicine in the different islands of Cape Verde. The Dicotyledons with 92 species constitute the highest number of plants used for medicinal purposes. Also nine Monocoty-

ledons were reported in our study. Most of these taxa are herbaceous, annual or biannual plants. However, some shrubs (e.g. *Vernonia colorata*, *Opuntia ficus-indica*, *Jatropha curcas*, *Lavandula dentata*, *Indigofera tinctoria*, *Sesbania grandiflora*, *Gossypium barbadense*, *Gossypium hirsutum*, *Ruta chalepensis*, *Capraria biflora*, *Lantana camara*), small trees (*Leucaena leucocephala*, *Sapindus saponaria*), and trees (*Tamarindus indica*, *Lonchocarpus laxiflorus*, *Melia azedarach*) have also been reported (table 1).

The present study revealed that the naturalized dicotyledonous species belonged to 28 families. The families with a greater number of medicinal species are the Fabaceae with fourteen species, the Asteraceae and the Malvaceae with twelve species each, the Amaranthaceae with eight species, and the Solanaceae with seven species (see table 1). The genera with the highest number of species are: *Sida* with four species; and *Amaranthus* and *Datura* with three species each. When referring to the monocotyledonous species naturalized in Cape Verde, of the five families with plants used in traditional medicine, the Cyperaceae is the family with more species, four taxa. On the other hand, concerning the Poaceae, which exists in large numbers in the archipelago (~ 120 grass species both native and exotic, see Duarte et al. 2008), only one species is referred to as being medicinal, *Imperata cylindrica* (table 1). Several other uses were registered for the grasses in Cape Verde, namely as pasture and foraging (data not shown).

The analysis of the non-naturalized exotic species with medicinal interest revealed that nineteen taxa belong to the medicinal flora of this archipelago. These taxa are distributed in ten families, of which eight are leguminous species (five Fabaceae and three Mimosaceae) (table 2). Most of these are woody perennial species, being mainly distributed across the islands of Santo Antão and Santiago, where the agricultural activity is higher.

Distribution of Cape Verde’s medicinal exotic plants

Regarding the worldwide distribution of the medicinal naturalized species (fig. 2) four main groups were observed: (a) Afrotropical species, of which the majority are from West

Table 2 – Checklist of the exotic cultivated medicinal plants of Cape Verde Islands.

(a), in the case of recent nomenclatural changes, synonyms commonly employed in Cape Verdean botanical literature are included; (b), the terminology used follows Morrone (2002). Whenever possible, the distribution of each taxon concerns to its native geographic range; (c), Cape Verde Islands abbreviations: A, Santo Antão; V, São Vicente; N, São Nicolau; S, Sal; B, Boavista; M, Maio; T, Santiago; F, Fogo; and Br, Brava.

family scientific name ^(a)	local name	native Distribution ^(b)	habit	distribution in Cape Verde ^(c)
Bombacaceae				
<i>Adansonia digitata</i> L.	calabaceira, caxabuceira	Afrotropical	tree	A, M, F
Crassulaceae				
<i>Kalanchoe daigremontiana</i> Raym.-Hamet & H.Perrier (= <i>Bryophyllum daigremontianum</i> (Raym.-Hamet & H.Perrier) A.Berger)	bálsamo	Afrotropical	perennial herb	A
Euphorbiaceae				
<i>Euphorbia tirucalli</i> L.	aveloz	Afrotropical- Oriental	shrub	S
<i>Manihot esculenta</i> Crantz	mandioca	Neotropical	shrub	A, V, N, S, B, M, T, F, Br
<i>Manihot carthagenensis</i> (Jacq.) Müll.Arg. subsp. <i>glaziovii</i> (Müll.Arg.) Allem (= <i>Manihot glaziovii</i> Müll.Arg.)	maniçoba	Neotropical	shrub	T
Lauraceae				
<i>Persea americana</i> Mill.	abacateiro	Neotropical	shrub or small tree	A, T, Br
Leguminosae (s. lat.)				
Fabaceae				
<i>Arachis hypogaea</i> L.	amendoim, mancarra	Neotropical	annual herb	T
<i>Canavalia ensiformis</i> (L.) DC.	fabatona, feijão-porco	Oriental	annual herb	T, Br
<i>Lablab purpureus</i> (L.) Sweet subsp. <i>purpureus</i>	feijão pedra, fixon	Oriental	annual herb	A, N, S, T, F, Br
<i>Lonchocarpus sericeus</i> (Poir.) Kunth ex DC.		Afrotropical- Neotropical	shrub or small tree	T, F
<i>Phaseolus lunatus</i> L.	n'bonge	Neotropical	annual or biennial herb	A, T, F, Br
Mimosaceae				
<i>Albizia lebbbeck</i> (L.) Benth.	coração-de-negro; pau-feijão	Oriental	tree	S, T, I
<i>Pithecellobium dulce</i> (Roxb.) Benth.	acácia-mineira	Neotropical	tree	F, Br
<i>Samanea saman</i> (Jacq.) Merr.	árvore-da-chuva; pau- feijão	Neotropical	tree	Br
Meliaceae				
<i>Trichilia roka</i> (Forssk.) Chiov. (= <i>Trichilia emetica</i> Vahl)	mafurreira	Afrotropical- Palaeartic	shrub or small tree	T
Myrtaceae				
<i>Eucalyptus camaldulensis</i> Dehnh.	calipro	Australotropical	tree	A, T, I
Punicacea				
<i>Punica granatum</i> L.	romã, romanzeira	Palaeartic	shrub or small tree	A, N, T, F, Br
Solanaceae				
<i>Nicotiana tabacum</i> L.	erva-brava, erva- santa, tabaco	Neotropical	annual or perennial herb	A, N, T, F, Br
<i>Solanum melongena</i> L.	beringela, beringelo, bringela	Oriental	annual or perennial herb	A, T

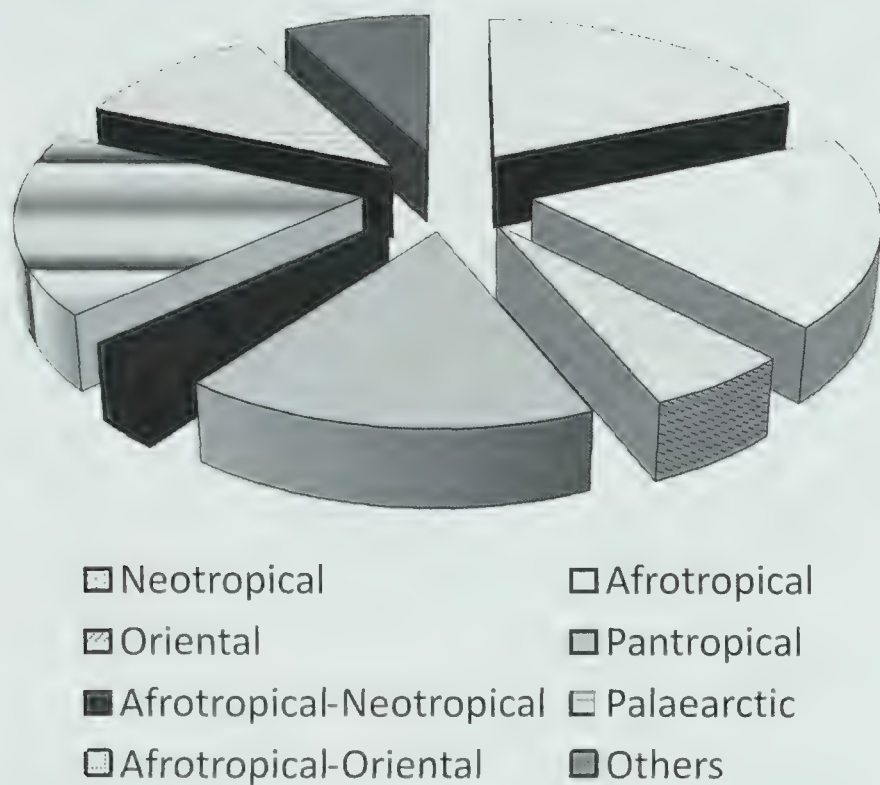


Figure 2 – Distribution of naturalized exotic species used in traditional medicine in Cape Verde Islands.

Africa (e.g. *Celosia trigyna*, *Heliotropium pterocarpum*); (b) Palaearctic species, many of which are from the Mediterranean region (e.g. *Lavandula dentata*, *Ruta chalepensis*); (c) Neotropical species namely from Brazil and Mexico such as *Datura inoxia* and *Leucaena leucocephala*; (d) and Pantropical species such as *Ageratum conyzoides*, *Momordica charantia*, *Clitoria ternatea*, and *Cyperus esculentus* (table 1). Among the species which are distributed between two biogeographical regions there is a predominance of the Afrotropical-Oriental.

From the analyses of the non-naturalized medicinal species used in traditional medicine of Cape Verde it was revealed that the majority are from Neotropical or Oriental (Asia) regions (fig. 3); on the other hand species from Palaearctic regions are not numerous, as opposed to what happens with naturalized medicinal species (see fig. 2). The predominance of the elements from Latin America and Tropical Asia is related to the fact that these are the places of origin and domestication of a large number of the species cultivated in the archipelago, like beans (*Canavalia ensiformis*, *Lablab purpureus* subsp. *purpureus*, *Phaseolus lunatus*), peanuts (*Arachis hypogaea*) or manioc (*Manihot esculenta*).

Half of the exotic medicinal species from Cape Verde (tables 1 & 2) is present in Guinea-Bissau (see Catarino et al. 2008), although it was found that only a reduced number are used as medicinal in both countries. For instance: *Abrus precatorius* (used for male impotence and tooth aches), *Spermacoce verticillata* (used for kidney problems and belly aches), *Chamaecrista absus* (to heal furunculosis and fever), *Chamaecrista nigricans* (used to treat wounds, as a purgative, and to treat worm problems), *Ocimum basilicum* (used to treat colds), *Senna occidentalis* (for venereal diseases, fevers or eye problems), are some of the species commonly used in the traditional medicine in Guinea-Bissau and Cape Verde Islands. Furthermore, many other species, used as me-

dicinal in Cape Verde, are referred to as alimentary (*Amaranthus spinosus*, *Amaranthus viridis*, *Adansonia digitata*), for phytochemical uses (*Acanthospermum hispidum*, *Indigofera tinctoria*), or for textile manufacturing (*Hibiscus cannabinus*, *Gossypium hirsutum*) in Guinea-Bissau.

DISCUSSION

As a result of human colonization and also of trading routes during the Age of Discoveries, most of the flora of Cape Verde archipelago is presently constituted by exotic naturalized species (Duarte & Romeiras 2009). The use of local flora in folk medicine is common in Cape Verde, and 101 exotic plants, i.e. about 20% of total exotic flora, were reported as medicinal in this archipelago. As a consequence of the hot and dry climatic conditions most of them correspond to annual or biannual herbs as with the overall flora.

Although, the introduction of useful plants in the Cape Verde Islands occurred at the same pace as their occupation (Barcellos 1899), for the 16th, 17th and the 18th centuries, there is no concrete information on medicinal plants used by the populations of this archipelago (Albuquerque 1991). One of the first descriptions of medicinal plants and how the local people used them in healing certain diseases was made by Feijó in 1797 (in Feijó 1986). Furthermore, in Filho (1995) an old description (from 1798) reported that an infusion of the leaves of the plant commonly named *fedegosa* (*Chenopodium ambrosioides*; see table 1) was used to help in labor, facilitating the uterine contractions: relaxation of the pelvic muscles and increase the resistance of blood vessels to prevent postpartum bleeding. According to Varela (1999, 2001), *C. ambrosioides* continued to be reported as an important medicinal plant with several applications in Cape Verde as well as in other tropical and subtropical areas. For instance, in Central and South America the leaves and flowers are presently used to stimulate labor, menses regulation and to treat abnormal uterine bleeding (Ososki et al. 2002), and in West Africa is used to stimulate blood flow in the pelvic area and uterus (Berhaut 1974). So, one of the most ancient descriptions about the traditional use of *C. ambrosioides* in the Cape

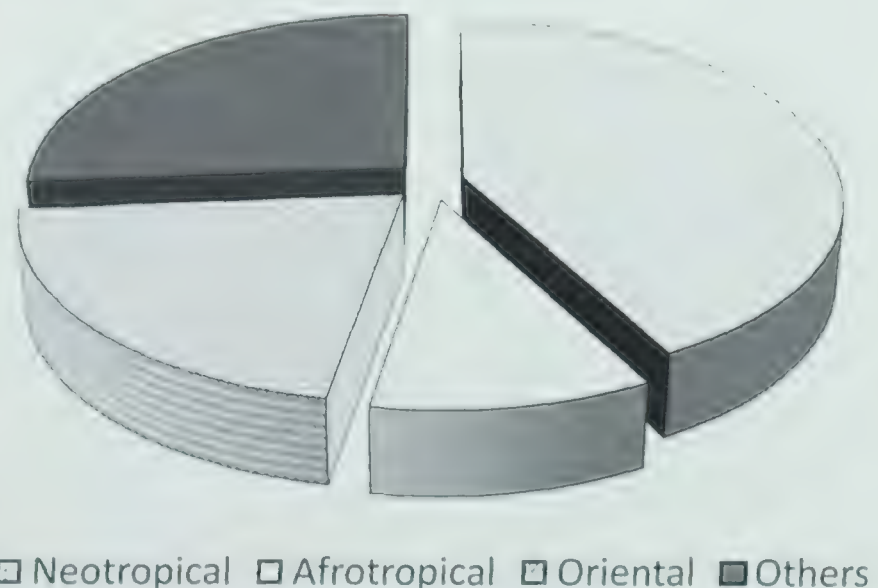


Figure 3 – Distribution of non-naturalized exotic species used in traditional medicine in Cape Verde Islands.

Verde Islands seems to reflect the current modern use of this plant in different parts of the world.

As it was noted, the position of these islands in the Atlantic Ocean allowed a rapid colonization, especially during the 18th–19th centuries. Several medicinal plants were introduced and adopted by Portuguese immigrants, although the traditional knowledge on the Cape Verde Islands was particularly influenced by African slaves. According to Torrão & Soares (2009), African slaves were subjected to severe workloads and unbearable living conditions and were forced to cure their own illnesses with local medicinal plants. These slaves, that initially colonized this archipelago or whilst en-route to Latin America, brought with them the knowledge of the uses of the local flora which is reflected in the predominance of elements Afrotropical and Neotropical highlighted in our studies. Regarding the exotic flora of Palaearctic distribution it is assumed that this is undoubtedly linked to the introduction of plants by the Portuguese during the whole process of colonization of the islands; species like *Foeniculum vulgare*, *Plantago major* or *Rosmarinus officinalis* are commonly used as medicinal in Portugal. Because of their economical interest, many of the plants were introduced by the Portuguese and other Europeans, which had in this way an important role in defining the composition of the flora of these islands. In this context, Ribeiro (1955) refers to Cape Verde as a centre of concentration and diffusion for plants, animals and men, as probably none other in the tropical regions; and Ferrão (1991) refers to the islands of Cape Verde as playing a role of extraordinary importance in the exchange of plants and worked as ‘gardens’ of acclimatization for plants from many places.

It was noted that the African slaves have certainly shaped the present day use of medicinal plants in the Cape Verde Islands, where the majority of the rural population still uses some plants to treat diseases. This comes as no surprise as the African continent has a long and impressive list of medicinal plants based on local knowledge (e.g. Burkill 1985, 1994, 1995, 1997, 2000, Schmelzer & Gurib-Fakim 2008). In Africa, traditional healers and remedies made from plants play an important role in the health of millions of people (e.g. Ayensu 1978). Every region has a form of traditional medicine, which varies from one community to another and is deeply rooted in a specific socio-cultural context (Oliver-Bever 1986, Rukangira 2001). For instance the roots and leaves of *Abrus precatorius* subsp. *africanus*, a tropical plant found in almost all of the West African countries are used in Cape Verde for conjunctivitis and skin diseases (Varela 1999, 2001). According to the Flora of Senegal (Berhaut 1976) this plant is widely used for broad applications such as: respiratory infections and cough; to cure anaemia; abortifacient. Meanwhile, in Guinea-Bissau, the dried root is used for “toothache and stomach aches”, and it is also understood to have an aphrodisiac effect (Catarino et al. 2006). Likewise, *Jatropha curcas* (Parawira 2010), a Euphorbiaceae described as medicinal in Cape Verde has an actual worldwide economic importance. This species is a drought-resistant perennial shrub, adapted to the arid and semi-arid conditions of all the Cape Verde Islands. The oil of its seeds can be combusted as fuel without being refined and used in folk medicine as a laxative or purgative (Figueiredo 1996).

The infant mortality in Cape Verde is among the very lowest in the West African region, the major health problems are related either with childhood diseases (e.g. diarrhoea, respiratory infections and cough), fevers, skin infections, urinary diseases or eye inflammations (Varela 1999, 2001). Most of these diseases are caused by poor hygiene, particularly the lack of treated water in rural areas. It is to be noted that Cape Verde has a relatively low prevalence of HIV/AIDS (Larsen et al. 1998), limited cases of malaria have been reported in Santiago Island, and tuberculosis appears only from time to time (Wessel et al. 1999) contrary to the other Sub-Saharan African countries. So, in Cape Verde the situation is not as serious as in other African countries; nevertheless, medical facilities in this archipelago are limited. For instance, there are only two central hospitals (in Mindelo, São Vicente Island and in Praia, Santiago Island); and Brava and Santo Antão no longer have functioning airports, and air evacuation, only by helicopters, is extremely difficult from these two islands. So, the cost of pharmaceuticals, the difficulty of reaching the two central hospitals, as well as limited availability of doctors, especially in the rural areas, most likely contributes to the widespread continued use of plants for medicinal purposes in this archipelago.

Finally, we would like to clarify that very few papers concerning aspects of the folk plant traditions have been published for Cape Verde Islands. Moreover interviews with traditional healers from these islands have scarcely been done and so, further field studies must be organized for a better characterization of the medicinal Cape Verde flora.

ACKNOWLEDGMENTS

We thank Ezequiel Correia for preparing the map of Cape Verde archipelago, and João Tavares which helped in the revision on the medicinal plants and their uses in Cape Verde. This work was supported by a grant (HC/0075/2009) from the Portuguese Science and Technology Foundation - FCT.

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- Manuscript received 12 Oct. 2010; accepted in revised version 19 Apr. 2011. This paper was pre-published on 15 Jun. 2011 in issue 144(2) of *Plant Ecology and Evolution*.
- Communicating Editor: Rainer Bussmann.



Agents and plants used in traditional medicine in the Orango Island (Guinea-Bissau)

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Background and aims – The Orango Island is included in the Bijagós Archipelago, Guinea-Bissau. The sanitary situation on this island is characterised by an almost absence of conventional medicinal care. In most cases traditional medicine is the only available recourse for local people to treat health problems and it plays an important role in basic health care. The purpose of this investigation was to document the medicinal use of local flora by traditional healers in the Orango Island.

Methods – A survey was made on the plants used by traditional medicine agents in Orango Island during the third quarter of 2007. Thirteen healers were indicated by the community as the best holders of traditional knowledge on the island. All of them agreed to participate and were inquired through semi-structured open-ended interviews.

Key results – Forty-six species of medicinal plants were referred, generally found near the villages. A total of 94 recipes were reported, from which 75 are different. The most common methods used in the preparation of traditional medicines are bark stripping, trituration, decoction, and maceration and the main administration ways are oral, topical, bath, and by inhalation.

Conclusions – Most of the medicinal uses of plants reported in Orango have been previously referred for other parts of the country and for West Africa but, at the local level, the knowledge on the medicinal properties of plants seems to be restricted to specific experts and is gender dependent. The collaboration between the traditional healers and other actors in the primary health care and the research on the properties of medicinal plants can be a way to add value to local knowledge and increase the services provided by natural resources to local populations.

Key words – Ethnobotany, ethnomedicine, healers, medicinal flora, West Africa, useful plants.

INTRODUCTION

In Guinea-Bissau, West Africa, the sanitary situation is characterised by a lack of qualified health workers, medicines and equipment. Infectious diseases, as malaria, AIDS, cholera, and tuberculosis are still common and are considered serious threats to public health (Larsen et al. 1998, Colombatti et al. 2009, Bjerregaard-Andersen et al. 2010). Because the access to conventional health care is often difficult, people use both conventional and traditional medicines to improve their health state. As in other African countries, traditional medicine, being an important element in the cultural patrimony, remains the main recourse for a large majority of people for treating health problems, particularly in remote areas (Rukangira 2001).

The traditional medicine encompasses the use of substances (herbs, plants, animals and mineral elements), dosages and practices based on sociocultural norms and religious beliefs as well as witnessed experiences and observation of a specific group, mainly traditional healers. This knowledge is handed down from generation to generation, in oral form (Inngjerdingen et al. 2004). The importance of traditional medicine for public health in developing countries is recognised by the World Health Organisation (Correa 2002).

There are about thirty different ethnic groups in Guinea-Bissau, each with their own practices, beliefs and ways of appropriation of natural resources. On the other hand, people use natural resources to satisfy most of their basic needs. So, there is in the country a deep knowledge about the properties of plants and their uses.

The first known study on the medicinal use of plants in the country was published by Costa (1895). It includes a list of medicinal plants, with vernacular names and preparation methods. Walter (1946) gives information on 41 species, including information on the vernacular names as well as chemical composition and other known uses. Espírito Santo, a collector with a deep knowledge of the country's flora, published two studies on the medicinal plants (Espírito Santo 1948, 1953). The more complete and extensive account on the medicinal flora of Guinea-Bissau was published by Vieira (1958). One hundred and sixty-eight vascular plant species used in traditional medicine are referred in this work, with vernacular names, methods of preparation and administration, as well as chemical composition and pharmacology, when known.

In the last decades, research on the ethnomedicine and ethnopharmacology of the country continued, both with fieldwork on the reported uses of plants (e.g. Gomes & Diniz 1993, Diniz et al. 1996, 2000, Martins et al. 1996, Gomes et al. 2003, Injai et al. 2010) and their pharmacological properties (e.g. Silva et al. 1996, 1997a, 1997b, 1997c, Abreu et al. 1999, Sousa et al. 2001, Silva & Gomes 2003, Silva 2004). Some work has also been made on the practical issues related to the use of plants in traditional medicine (e.g. Mencagli 1992, Caritas Guine-Bissau 2004).

Based in the herbarium specimens from Guinea-Bissau held at LISC herbarium, Catarino (2004) reported the medicinal use of 201 species in the country, from which 180 are autochthonous and 21 introduced.

The purpose of this investigation was to document the medicinal uses of local flora by traditional healers in the Orango Island, identifying the plants used, their reported properties and the methods of preparation and administration.

MATERIAL AND METHODS

Study area

The Bijagós Archipelago comprises about forty islands and is located near the coastline of Guinea-Bissau, West Africa. Orango Island is included in the Bijagós Archipelago, and lies between 11°01'–11°13'N and 16°03'–16°15'W. It is the largest of the five islands of the Orango National Park, which has a surface area of 1582 km² (fig. 1).

In 2007 there were 3369 inhabitants living in 33 villages in Orango, belonging almost entirely to the Bijagós ethnic group, with animistic beliefs (INEP/INEC 2007).

Due to its isolation from the continent, the sanitary situation in this island is characterised by an almost absence of conventional medical care. In most cases traditional medicine is the only available recourse for local people to treat health problems and plays an important role for basic health care.

The known flora of Bijagós Archipelago consists in about 450 taxa (Catarino 2004, Catarinao et al. 2008), but this figure can be underestimated since it is based only in the herbarium specimens collected on the islands. The vegetation of Orango Island consists mainly in savannah woodland, woodland, palm groves of *Elaeis guineensis* and mangroves.



Figure 1 – Location of the Orango Island in Guinea-Bissau and villages in which the fieldwork was done.

According to Teixeira (1962) the prevalent soils in the upper lands are Arenosols, occupied mainly by savannah woodlands, and Ferralsols, where the natural vegetation is mainly composed by palm groves and woodlands. In the shoreline, Fluvisols extend over large areas, and are predominantly occupied by mangroves.

The climate has two contrasting seasons: a long dry season, with almost no rainfall, from November to May, and a rainy season of five months from June to October. The annual rainfall in Orango is c. 2200 mm and the average annual temperature is c. 26°C (Machado 1972).

The main economic activities in the island are fishing and shifting agriculture and the main food crop is upland rice, cropped by the slash-and-burn system. Nevertheless, in the last decades, cashew plantations became another important economic activity. In recent years there was also some development in tourism, linked mainly to the observation of hippopotamus, and a little hotel was opened near Eticoga.

Data collection and analysis

A survey was made on the plants used by traditional medicine agents in Orango Island during the third quarter of 2007. Prior to the fieldwork campaign, the script to the semi-structured, open-ended interviews was designed and tested in Bissau. At the beginning of the fieldwork campaign, a meeting was held between the researchers, Orango National Park staff members, and local community leaders, in order to: i) explain the aim of the work and its integration in the Park activities; ii) get cooperation and permission to use the cultural heritage of Bijagós people; iii) select the informants according to their level of knowledge, age and gender; and iv) plan the field activities.

Thirteen healers (ten men, three women) were indicated by the community as the best holders of traditional knowledge in the island. All of them agreed to participate and were inquired through semi-structured, open-ended interviews. The interviews were performed in Creole, the vehicular language in the country. When needed, the translation to Bijagó, the language of the Bijagós ethnical group, was made with the support of the Orango Park staff.

Herbarium vouchers from the plants referred were made during the fieldwork campaign, for later identification. A set of the plants collected is kept at LISC herbarium (Tropical Research Institute, Lisbon, Portugal). A photographic record of the campaign was made, including all the healers and the plants referred.

The identification of plant species was made using the available bibliography, namely Flora of Senegal (Berhaut 1971–1979; Vanden Berghen 1988) and flora of West Tropical Africa (Hutchinson & Dalziel 1954–58, Hepper 1963, 1968–72), as well as through comparison with the specimens from the country held at LISC herbarium. The nomenclature follows the African Plants Database (2010).

RESULTS

The medicinal flora of Orango

Forty six species of medicinal plants were referred, from 28 families and 43 genera, about one tenth of the known flora of the Bijagós Archipelago. Twenty-three of the species used are trees, fifteen are shrubs, six are herbs and two are lianas (see table 1). The families most represented in the medicinal flora of Orango are the Euphorbiaceae, with four species, and the Combretaceae, Caesalpiniaceae and Rubiaceae with three species each.

Thirty-eight species are native and eight are introduced. From these, four are trees cultivated for its fruits: *Anacardium occidentale* (cashew), *Carica papaya* (papaya), *Citrus limon* (lemon), and *Mangifera indica* (mango). *Luffa cylindrica*, *Ocimum basilicum* and *O. gratissimum* are sub-spontaneous herbs, formerly cultivated, and *Jatropha curcas* is a shrub planted as a living fence.

The plants used with medicinal purposes are generally found near the villages, mainly in forest regrowths and in cultivated land. According to the Orango healers, the species used in traditional medicine are in general easy to find near their villages. The populations of most tree and shrub species are said to be increasing, and this is attributed to the regrowth of forest vegetation due to the decrease of slash-and-burn agriculture. Nevertheless, some species are becoming rarer: *Citrus limon* and *Combretum micrantum* are said to be dying due to the decrease in rainfall. The same goes for *Faidherbia albida* because its wood is used to make tools; *Prosopis africana*, because it is cut to make charcoal; and *Strophanthus sarmentosus*, because of the intensive use of its roots.

The medicinal uses of plants in Orango

A total of 94 recipes were reported, from which 75 are unique. In most cases each species is referred for one or two recipes. Conversely, each recipe was referred by up to four healers,

but the more common situation is the report of each recipe by a single healer.

In fig. 2 the references found in bibliographic sources for the medicinal species used in Orango Island are quantified. The same use was previously reported in the country for half of the Orango medicinal species and for about seventy percent of the species in West Africa. A large part of the species has also other medicinal uses reported, both in the country (c. 85%) and in the neighbouring countries, in which more than ninety percent of the species referred by the Orango healers have been previously reported.

Pains are the condition for which more recipes are referred, in a total of seventeen, followed by the diseases of newborns and women, related to pregnancy and childbirth, which are treated with sixteen recipes. The intestinal problems, mainly diarrhoea and abdominal pains, are the subject of twelve recipes. In skin problems, for which ten recipes were referred, inflammation and infections in various parts of the body are the most common. Fevers, cough and malaria are treated by seven potions, but it is sometimes difficult to ascertain the origin of the fever. Bites and poisoning are treated by seven recipes, most of them for snake bites. The remaining seven recipes address a wide range of diseases: mental disorders, neuromuscular problems, gonorrhoea, male impotence, loss of appetite, hepatitis and hypertension. The correlation between each disease reported by the healers and the classification of diseases of official medicine is sometimes difficult to establish. It is the case for instance of ‘baça’, a disease of the newborn, for which we cannot find the corresponding name.

Plant material used

Leaves, roots and stem bark are the plant parts mostly used as components in recipes (table 2). Leaves (including young leaves) are used alone as the basis of 22 recipes, and combined to stem bark or roots of the same plant in thirteen recipes. Roots are used in a total of 27 recipes and stem bark in twenty. If the medicinal species is a herb, all the aerial part of the plant can be used (five recipes). Fruits and apical buds are used in one recipe each.

In two thirds of the recipes only material from one plant species is used and in 25 recipes there are two or more components associated. These are mainly other plants or plant parts, used in eleven recipes, as well as salt, in six, and palm oil in five. Several other components are used in a recipe each (table 2).

Preparation and administration methods

The preparation of traditional medicines from the plant material can be done in several ways and often includes more than one procedure (fig. 3). The most common methods used are bark stripping, trituration, decoction, and maceration. Other procedures are drying and heating, and less often burning, chewing, peeling or squeezing. Water is used whenever the preparation of a recipe is made using a liquid, mainly in decoction and maceration procedures. In two recipes, the plant material is used directly, without previous manipulation.

The ways of administration depend on the nature of the disease or condition to treat. Oral administration (mainly by

Table 1 -- Medicinal plant species used in Orango Island.

Habits: H = herb; L = liana; S = shrub; T = tree. Key to the languages of vernacular names: bj = Bijagó; cr = Creole. Key to the references for uses in Guinea-Bissau: A – Costa 1895; B – Walter 1946; C – Espírito Santo 1948; D – Espírito Santo 1953; E – Vieira 1958; F – Gomes & Diniz 1993; G – Martins et al. 1996; H – Diniz et al. 2000; I – Gomes et al. 2003; J – Catarino et al. 2006. Key to the references for uses in West Africa: 1 – Ayensu 1978; 2 – Burkhill 1985–2000; 3 – Oliver-Bever 1986; 4 – Schmelzer & Gurib-Fakim 2008.

Species	Family	Vernacular names in bijagó (bj); crioulo (cr)	Habit	Orango Island uses	Plant parts used / Preparation / Administration	Same use in GB / W. Afr.	Other uses GB / W. Afr.
<i>Albizia leucodermis</i> subsp. <i>africanus</i> Verdc.	Labaceae	ovocate (bj); planta-di- açucar (cr)	L	“baça” of children	leaves / trituration, maceration / drink	1	B, E, H, J / 2, 1, 3
<i>Adansonia digitata</i> L.	Bombacaceae	uvato (bj); Cabaceira (cr)	T	childbirth facilitator	leaves / trituration, maceration / drink		A, B, E, F / 2, 3
<i>Albizia leucodermis</i> P.Beauv.	Sapindaceae	epec (bj); três-folhas (cr)	S	skin inflammations, itch	leaves / decoction / bath	2	E / 3
<i>Anacardium occidentale</i> L.	Anacardiaceae	cadju (bj); cadju (cr)	T	headache	leaves / direct and decoction / direct and bath	H / 2	B, E, H, J / 2, 3
<i>Annona senegalensis</i> Pers.	Annonaceae	ebud (bj), pinha-di-mato, mambumba (cr)	S	headache abdominal pain	leaves / trituration / inhalation and plasters leaves / decoction / drink	A, E / 2	B, E, J / 2
<i>Antiaris toxicaria</i> Vogel Planch.	Loganiaceae	cadjanué, ghodegha (bj), tabaco-di-lubo (cr)	T	earache constipation	apical bud / heat / topical stem bark / decoction / eaten	2, 3, 4	2, 4, 3
<i>Buddleia maurandia</i> (Hochst.) Baill.	Euphorbiaceae	ghuntague (bj), bissaca (cr)	T	diarrhoea constipation	roots / peeled, trituration and maceration / eaten roots / peeled, decoction / drink	J / 1	E, G, J / 1
<i>Calyptranthes</i> <i>Christianum</i> (Rehder) Summerh	Orchidaceae	capoquepanha (bj), orquídia (cr)	H	back pain	whole plant / decoction / bath	2	J / 2
<i>Capparis erythrocarpus</i> Isert	Capparaceae	etchãcane (bj), fidida (cr)	S	headache	roots / peeled, trituration / inhalation	J / 1, 2	J / 2, 1
<i>Carica papaya</i> L.	Caricaceae	ghopadanga (bj), pé-di- papaia, papaia, papaia- matcho (cr)	F	childbirth facilitator	leaves / trituration, maceration / drink	E	B, E, G, J / 2, 3
<i>Cassytha filiformis</i> L.	Lauraceae	udanva (bj), ridia-di- santehu (cr)	H	childbirth facilitator	aerial part of plant / trituration, maceration / drink		E, J / 2
<i>Cissampelos mucronata</i> A.Rich.	Menispermaceae	cabotche(bj), oredja- di-rato, orelha-de-rato, oredja-di-sanjo (cr)	L	abdominal pain	roots / peeled, trituration, maceration / drink	B, E / 2, 4	B, E, J / 1, 2, 3, 4
<i>Citrus limon</i> (L.) Burm.f.	Rutaceae	essagara-edjoco (bj), limon-di-terra, limon (cr)	T	headache diarrhoea	roots and leaves / peeled (roots), trituration / inhalation and plasters roots and leaves / peeled (roots), decoction / drink	2	A, J / 2

Table 1 (continued) -- Medicinal plant species used in Orango Island.

Species	Family	Vernacular names in bijagó (bj); crioulo (cr)	Habit	Orango Island uses	Plant parts used / Preparation / Administration	Same use in GB / W. Afr.	Other uses GB / W. Afr.
<i>Cnestis ferruginea</i> DC.	Connaraceae	nerogo (bj), udju-di-onça (cr)	S	inflammation, swelling stomach pain	leaves / trituration, heating / plasters roots / peeled / chewed	E, J / 2, 1	H, J / 2, 1
<i>Combretum mucronatum</i> G. Don	Combretaceae	epueque (bj), buco (cr)	S	earache wounds burns	fruits / heat, squeeze / topical roots / peeled, chewed / plasters leaves / decoction / bath	E / 3	B, E, G, J / 2, 3
<i>Elaeis guineensis</i> Jacq.	Palmae	erara (bj), palmera (cr)	T	male impotence female infertility	roots / peeled, decoction / drink stem bark and roots / peeled, maceration / drink	E, F / 2	
<i>Erythrina senegalensis</i> DC.	Fabaceae	cusserum (bj), dolin (cr)	T	“baça” of children ray bite	stem bark / peeled, trituration, maceration / drink stem bark / trituration, heating / plasters	2	E, F, I / 2
<i>Faidherbia albida</i> (Delile) A.Chev.	Mimosaceae	camudo (bj), fidida-branco (cr)	T	inflammation, swelling	stem bark / peeled, dry, decoction / drink		2
<i>Ficus exasperata</i> Vahl	Moraceae	noi (bj), po-di-lixá (cr)	T	gonorrhoea	stem bark / peeled, decoction / drink	2	E / 2
<i>Ficus polita</i> Vahl	Moraceae	canhimva (bj), figuera, figueirinha (cr)	T	childbirth facilitator	leaves and stem bark / trituration, maceration / drink		
<i>Guiera senegalensis</i> J.F.Gmel.	Combretaceae	cararé (bj), badodoce (cr)	S	bronchitis skin inflammations	roots and leaves / peeled, decoction / drink leaves / decoction, trituration / bath and topical	A, B, E / 2, 3	B, E, F, H, I, J / 2, 3
<i>Hymenocardia acida</i> Tul. var. <i>acida</i>	Euphorbiaceae	netchondor, netendor (bj), coroncondo (cr)	S	body pains female infertility	roots / peeled, maceration / drink leaves / decoction / inhalation	G / 2, 4	B, E, F, J / 2, 4
<i>Latrophia curatás</i> L.	Euphorbiaceae	ghorok (bj), pulga (cr)	S	snake bite	roots / peeled, trituration, maceration / drink	2	A, E, J / 1, 2, 3, 4
<i>Khaya senegalensis</i> (Desf.) A.Juss.	Meliaceae	ussonro (bj), bissilon (cr)	T	cough	stem bark / dry, peeled, maceration / drink		A, B, E, G / 2, 3
<i>Landolphia dulcis</i> (R.Br. ex Sabine) Pichon	Apocynaceae	eropod (bj), fole (cr)	L	lack of appetite and stomach pain	roots / dry, peeled, trituration / eaten	C, E, J	J / 2
<i>Leptadenia hastata</i> (Peters.) Vatke	Asclepiadaceae	caido (bj), cibode (cr)	L	wounds lack of milk (lactation stimulant)	sap and leaves / direct and trituration / topical and plasters stem and leaves / trituration, maceration / drink	2	A, E, J
<i>Luffa cylindrica</i> (L.) M.Roem.	Cucurbitaceae	esenquedjaque (bj), pipino-di-lubo, djadar (cr)	H	diarrhoea	leaves / trituration, maceration / drink		2

Table 1 (continued) -- Medicinal plant species used in Orango Island.

Species	Family	Vernacular names in bijagó (bj); crioule (cr)	Habit	Orango Island uses	Plant parts used / Preparation / Administration	Same use in GB / W. Afr.	Other uses GB / W. Afr.
<i>Mangifera indica</i> L.	Anacardiaceae	mango(bj), pé-di- mango(cr)	T	toothache	root / decoction / inhalation	2, 3 / J	G, H, J
<i>Margaritaria discoidea</i> (Baill.) Webster var. <i>discoidea</i>	Euphorbiaceae	ghossaba (bj)	S	neuromuscular problems diarrhoea malaria	leaves / decoction / inhalation and bath leaves and stem bark / peeled, decoction / drink leaves and stem bark / peeled, decoction / bath	2	2
<i>Morinda geminata</i> DC.	Rubiaceae	ghobonodo, obonodje (bj), bulongodjiba (cr)	S	postpartum recovery	leaves / dry, decoction / bath and drink	E, G, H, I, J / 2	A, E, H, I, J / 2
<i>Neocarya macrophylla</i> (Sabine) Prance ex J. White	Chryso- balanaceae	Urudo (bj), tambacumba (cr)	T	burns toothache abdominal pain	leaves / burn / topical stem bark / decoction / inhalation stem bark / peeled, maceration / drink	2	J / 2
<i>Newbouldia laevis</i> (P.Beauv.) Seem.	Bignoniaceae	ghossonconco (bj), manduco-di-futucero (cr)	T	fever	roots and leaves / peeled (roots), trituration, maceration / bath	E / 2	C, E, J / 1, 2, 3
<i>Ocimum basilicum</i> L.	Labiatae	puaré (bj), mancircon, menzinho-di-bitchu (cr)	H	skin inflammations	aerial part / decoction / bath	1	J / 1, 3
<i>Ocimum gratissimum</i> L.	Labiatae	ghobongongo (bj), doreda (cr)	S	fever headache	aerial part / trituration, maceration / bath and drink leaves / direct / plasters	E / 1, 2, 3	E, J
<i>Parinari excelsa</i> Sabine	Chryso- balanaceae	nhêg-cuneme, uguene, ukenim, uquenon (bj), mampataz (cr)	T	“baça” of children body pains	stem bark / peeled, maceration / drink stem bark / peeled, trituration / ointment	2	E, J / 2
<i>Ptilostigma thommingii</i> (Schumach. & Thonn.) Milne-Redh.	Caesalpiniaceae	nepanrambu (bj), pano-di- kankora (cr)	T	diarrhoea	roots / peeled, decoction / drink	B, E	B, E, F, G, I, J / 2
<i>Prosopis africana</i> (Guill. & Perr.) Taub.	Mimosaceae	coquengue (bj), pau- carvão, pó-carvão, po-de- carbom,po-di-carvom (cr)	T	female infertility toothache	roots / peeled, maceration / drink leaves and stem bark / decoction / inhalation	2	F / 2
<i>Psychotria peduncularis</i> (Schnell) Verdc.	Rubiaceae	ghupughe (bj), po-di-bras (cr)	S	hypertension snake bite poison antidote	leaves / decoction / drink roots / peeled / chewed roots / decoction / drink	H / 2	H, J / 2
<i>Sarcocephalus latifolius</i> (Sm.) Bruce	Rubiaceae	canhaminha (bj), caboupa, madronha (cr)	S	postpartum recovery	roots and leaves / peeled (roots), decoction / drink and bath		A, B, F, G, H, I, J 2, 3

Table 1 (continued) – Medicinal plant species used in Orango Island.

Species	Family	Vernacular names in bijagó (bj); criole (cr)	Habit	Orango Island uses	Plant parts used / Preparation / Administration	Same use in GB / W. Afr.	Other uses GB / W. Afr.
<i>Senna occidentalis</i> (L.) Link	Caesalpiniaceae	necepo (bj), padja-santa, palha-santa (cr)	S	fever body inflammations	leaves / maceration / bath and drink leaves / trituration, maceration / drink	A, B, E, J / 2	B, E, J / 2
<i>Senna podocarpa</i> (Guill. & Perr.) Lock	Caesalpiniaceae	necepo, negonoghate-oreboc (bj), palha-santa, planta-di-regulo (cr)	S	female infertility constipation	leaves / trituration, maceration / drink roots and leaves / peeled (roots), trituration, decoction / drink	I / 2, 4	I / 2, 4
<i>Strophanthus sarmientosus</i> DC. var. <i>sarmientosus</i>	Apocynaceae	manate, unucan-iinrighaghe (bj), cuntés (cr)	S	hepatitis	roots / peeled, maceration / drink		B, E, J / 2
<i>Terminalia macroptera</i> Guill. & Perr.	Combretaceae	uqueredjo (bj), massite (cr)	T	anti-abortion body pains	leaves / decoction / drink stem bark / peeled, trituration / plasters	E	B, D, E, F, I, J / 2, 3
<i>Trichilia prieuriana</i> A.Juss. subsp. <i>prieuriana</i>	Meliaceae	cudaco, nequeno (bj)	T	snake bite	stem bark / peeled, maceration / drink	J	I
<i>Lavaria chamac</i> P.Beauv.	Annonaceae	edjotchotche (bj), banana-santchu (cr)	S	snake bite mental disorders flu	leaves and root bark / peeled (root), trituration, maceration / drink leaves and roots / peeled (root), trituration, decoction / bath leaves / decoction / inhalation	E / 2	B, E, J / 2, 1, 3
<i>Zanthoxylum lepreurii</i> Guill. & Perr.	Rutaceae	cranha (bj)	T	snake bite abdominal pain	stem bark / trituration / eaten, powder roots and leaves / peeled (roots), trituration / maceration / drink	H, J / 2	H, I, J / 2

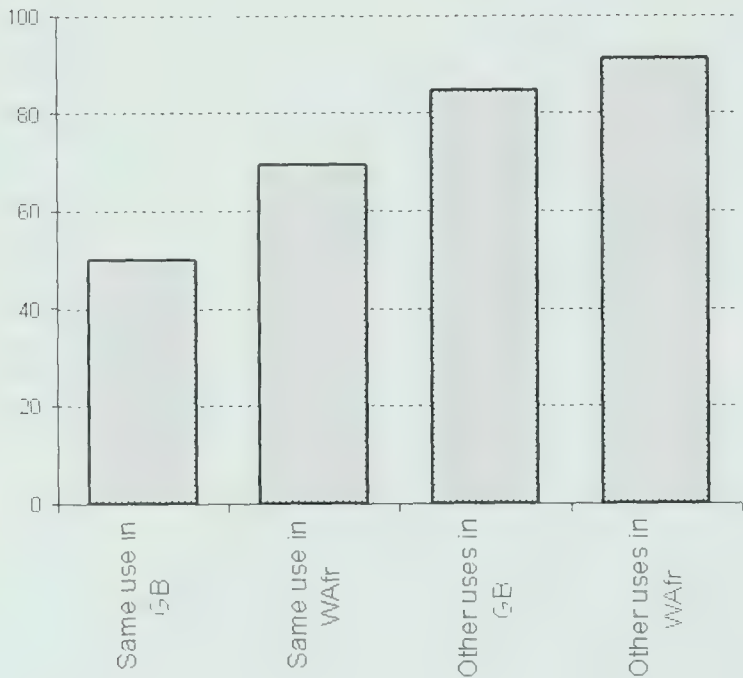


Figure 2 – Reported uses in Guinea-Bissau (GB) and West Africa (WAfr) for the Orango medicinal plants.

drinking, but also eaten and chewed) is the most used, accounting for 42 recipes, followed by topical administration in ten cases (often plasters), bath in six and inhalation in five (fig. 4). On ten recipes, administration is applied in more than one way, often bath and oral administration.

DISCUSSION

In the present study 46 species belonging to 28 vascular plant families have been identified as applied in traditional remedies in Orango Island, most of them are a part of the autoch-

Table 2 – Plant parts used as main components of recipes and other components used.
(The total of recipes with associated components is different to the sum of recipes with other components because some recipes have two or more associated components.)

Plant parts used as main components	Recipes
Leaves	22
Roots	19
Stem bark	14
Fruit	1
Apical bud	1
Aerial part	5
Roots and leaves	7
Stem bark and leaves	5
Stem bark, roots and leaves	1
Other components used	
Other plants	11
Salt	6
Palm oil	5
Other products ('black soap', garlic, peanuts, onion, perfume, ray, rice flour, sugar)	8
Total of recipes with associated components	25

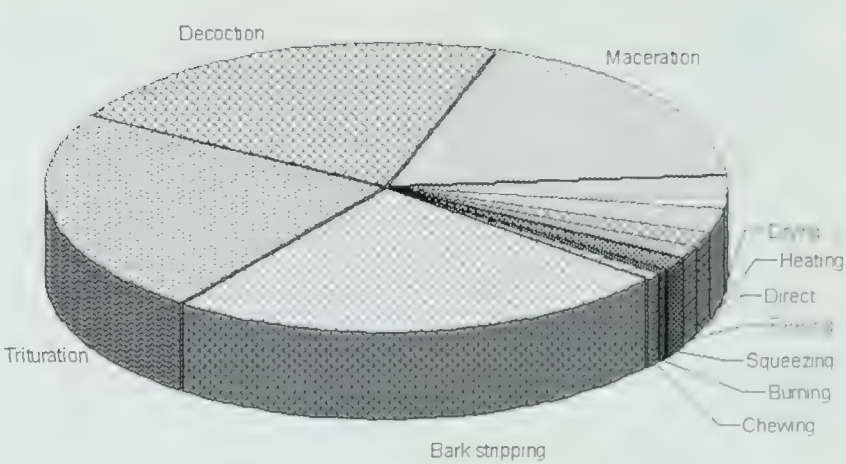


Figure 3 – Preparation methods used.

thonous flora. The majority of the diseases treated are pains, problems related to pregnancy, childbirth and newborn diseases, intestinal problems, and skin inflammations, wounds and burns. Other groups of diseases with several recipes are cough, fever and malaria, and stings, bites and poisoning. However, in some cases there are difficulties in making the correspondence between the conditions and diseases reported by traditional healers and the ones described in conventional medicine. This can be related to different views and perceptions of the origins and manifestations of the body imbalances related to the diseases.

The possession and transmission of knowledge about the properties of plants seems to be gender dependent in Orango. Most of the healers recognised as such by the community are men, while women are in charge of children, pregnant and woman healthcare.

In most cases, the medicinal uses of plants referred in Orango have been previously reported in other parts of the country and in West Africa. Nevertheless, a large majority of plants and recipes were referred by a single or two healers. So, even when the knowledge of the medicinal properties of plants is widespread in the country or abroad, at local level the possession of knowledge on the medicinal properties of plants seems to be restricted to experts and probably viewed as a wealth, and is not broadly spread.

The medicinal plants used in Orango are in general easy to find in the island and their populations are said to be stable or increasing in the last years. Only five species are referred

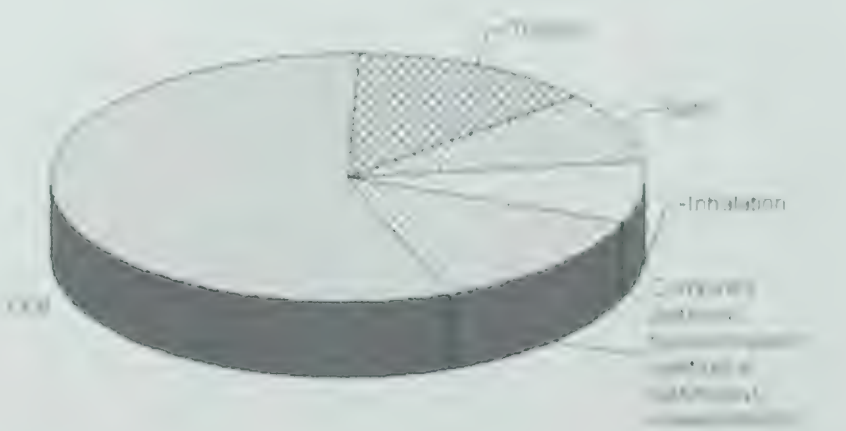


Figure 4 – Administration methods used

as having a decrease in their populations through time. *Strophanthus sarmentosus* is the only one that can be rarer at present because of the intensive medicinal use. In such a case of useful species intensively used, the domestication or the protection of the plant populations can be ways for its conservation (Cunningham 1993).

In an isolated area with very limited access to the conventional medicine, such as the Orango Island, traditional medicine plays an important role in the well being of human populations. The collaboration between traditional healers, health care staff and other actors in the primary health care, such as the religious missions and non governmental organizations, can also be a way to improve and spread the knowledge on the medicinal usage of local flora. The work of Crowley & Ribeiro (1987) on the ways of collaboration between traditional and modern medicine must be a reference to the country, as well as the manuals of recipes on the medicinal use of plants made by Mencagli (1992) and Caritas Guiné-Bissau (2004).

The demonstration of bioactivity of plant extracts, which corresponds to its traditional application, can support the traditional medical use of the plants and provide efficient and non-toxic medicines to the population. On the other hand, further phytochemical, pharmacological and toxicological studies of the plants identified during the ethnobotanical surveys can be a way to improve the safe and wise use of medicinal plants and perhaps to isolate new active substances (Ayensu 1978).

Nevertheless, it should be noted that some medicinal plants used in Orango Island, such as *Jatropha curcas* and *Cnestis ferruginea*, are reported to be toxic. *J. curcas* is reported as a common cause of accidental poisoning, namely among children, and feeding studies showed severe clinical and pathological symptoms in several animal models (e.g. Li et al. 2010). Gastrointestinal manifestations are predominant feature of poisoning with their seeds (Kumar & Sharma 2008). This kind of symptoms was not reported as a reaction to the drug administration in Orango in our study, but there is notice of the poisoning of at least two children in Bissau caused by the ingestion of *J. curcas* nuts (B. Injai, pers. comm.). *C. ferruginea* has several medicinal uses reported in West Africa but it is known also to have harmful effects. In a study made in Casamance (Senegal) by Garon et al. (2007) poisoning by neurotoxic compounds from this plant was reported to be the cause of more than fifty deaths. Even if there is no report of such effects in Orango Island and in Guinea-Bissau, the potential toxic effects of these and probably some other plants show that the use of medicinal plants is not free of risk and their properties must be studied in order to promote their safe use.

Research on the properties of medicinal plants and establishment of standard procedures for preparation, administration and doses, is being done in some West African countries (e.g. Etonde & Malobe 2003, Togola et al. 2005). This kind of work can also be done in Guinea-Bissau which has a large diversity of ethnical groups with different approaches to the use of natural resources. The research on ethnobotany in the country can be a way to value local knowledge and contribute to put natural resources at the service of local populations.

ACKNOWLEDGEMENTS

The fieldwork in Orango Island was made by Bucar Injai with the financial support of the Institute for Biodiversity and Protected Areas (IBAP) of Guinea-Bissau through a paid consultancy. The collaboration of Dora Mourão in this work was supported by a research fellow from the Portuguese Foundation for Science and Technology (FCT) (fellow IICT-CAI-JBT-8). We are deeply grateful to the Orango healers that collaborated in the study for all the cooperation received and the trust placed on us. Their names are: Augusto Fernandes Pereira, Augusto Utomb, Joana Monteiro, João Iatebeto, Joaquim Pereira, Joaquim Unhamaque, José Obassene, José Vieira Mandinga, Muscuta da Silva, Ramalho do Reno, Raul Iaratano, Rosa Cugussamé, and Silva Martins. We are grateful to the IBAP leaders and staff in Bissau, namely Alfredo Simão da Silva, Justino Biai, João Sousa Cordeiro, and Cristina Silva, for their support before and after the fieldwork campaign; and to the IBAP staff members in the Orango Park António da Silva, Augusto da Silva, Domingos Alves Júnior and Salvador Joãozinho Utebanico for their support during the fieldwork campaign.

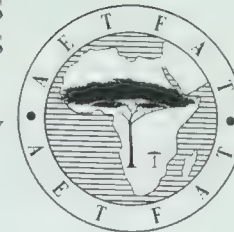
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Manuscript received 16 Sep. 2010; accepted in revised version 10 Jan. 2011.

Communicating Editor: Rainer Bussmann.



Valeurs socioculturelles et gestion de la diversité génétique d'*Elaeis guineensis* (Arecaceae) en République du Congo

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Sociocultural values and genetic diversity management of *Elaeis guineensis* (Arecaceae) in the Republic of Congo

Background – This ethnobotanical study shows the social values associated to the *Elaeis guineensis* morphotypes, virescens and albo-virescens fruits essentially, and the management of the species' genetic diversity in the Republic of Congo.

Methods – Normal practises of ethnobotany studies have been applied.

Key results – This work is founded on the sociocultural values of *Elaeis guineensis* which is a multi-purpose plant. Its value and virtues are known and exploited, as well by the populations of its origin area as by those of its extension area. In spite of this good knowledge and exploitation of the species, specificities associated with the morphotypes with the virescens, albo-virescens and albo-nigrescens fruits, are observed in Republic of Congo. In connection with empirical considerations and taboos related to the food, medicinal and magicotherapeutic (exoteric and esoteric practices) properties they represent sometimes an undeniable sociocultural value for the traditional society. The investigations having carried into several groups ethnic/linguistic, the perception of the virescens and albo-virescens fruits are different between them. In comparison of manners associated to the virescens, albo-virescens and albo-nigrescens fruits, the morphotypes with the virescens and albo-virescens fruits are more particularly concerned by an intentional eradication on behalf of the ethnic/linguistic groups studied.

Key words – Republic of Congo, *Elaeis guineensis*, multiple uses, empirical considerations, manners, survival of the populations, genetic diversity.

Contexte – Cette étude ethnobotanique montre les valeurs sociales associées aux morphotypes d'*Elaeis guineensis*, notamment à fruits virescens et albo-virescens, et la gestion de sa diversité génétique en République du Congo.

Méthodes – Les méthodes classiques de recherches ethnobotaniques ont été utilisées.

Résultats-clés – Ce travail est fondé sur les valeurs socioculturelles d'*Elaeis guineensis* qui est une plante à usages multiples. En dépit de l'exploitation commune des valeurs et vertus par les populations de son aire d'origine et d'extension, des spécificités associées aux morphotypes aux fruits virescens, albo-virescens et albo-nigrescens, sont observées en République du Congo. Ces considérations empiriques et ces interdits liés aux propriétés alimentaires, médicinales et magicothérapeutiques (pratiques exotériques et ésotériques) représentent souvent une valeur socioculturelle indéniable pour les sociétés traditionnelles. Les enquêtes ayant porté sur plusieurs groupes ethniques/linguistiques, la perception des fruits virescens et albo-virescens est différente entre eux. L'analyse des mœurs associées aux fruits virescens, albo-virescens et albo-nigrescens, montre que les morphotypes aux fruits virescens et albo-virescens sont plus particulièrement concernés par une éradication intentionnelle de la part des groupes ethniques/linguistiques étudiés.

INTRODUCTION

Elaeis guineensis Jacq. est une espèce intimement liée à l'histoire des sociétés humaines du golfe de Guinée (Nitza 1984, Comte 1991, Fleury 1994, Cunningham 1997). Souvent et voire toujours, elle caractérise l'anthropisation du milieu. Le genre *Elaeis*, distribué en zone tropicale afro-américaine, est représenté par deux espèces nettement distinctes: *E. guineensis* en Afrique et *E. oleifera* (Kunth) Cortés en Amérique. *E. guineensis* compte une sous-espèce et une variété (Cornet 2001). Les données taxonomiques rapportent le genre *Elaeis* à la sous-famille des Cocoideae, et à la famille des Arecaceae (APG III 2009, Cornet 2001, Judd et al. 1999, Mabberley 1993). Cependant, une revue de la littérature systématique sur *Elaeis guineensis*, montre que plusieurs tentatives visant à circonscrire le rang taxinomique de la variabilité observée chez cette espèce n'ont pas abouti. En effet, pour non observation du code de nomenclature, les résultats des travaux de classification de Chevallier (1910) et Beccari (1914) intéressant l'attribution d'un rang taxinomique (sous-espèces, variétés, forma, ...) à toutes les unités de cette variabilité ont été invalidés. En conséquence, l'invalidation de toutes les combinaisons proposées et la difficulté d'attribuer un niveau systématique qui fasse l'unanimité, l'usage de termes comme "taxa, type, variété, sous-espèce..." est exclu au profit de "morphotype". Au stade actuel des connaissances sur la taxonomie de *E. guineensis* et de toute la variabilité qui l'entoure, il n'est pas aisé de se prononcer sur tel ou tel niveau systématique. Ainsi, nous traiterons des morphotypes *E. guineensis* aux fruits virescens, albo-virescens, albo-nigrescens et nigrescens, même si la littérature la plus récente associe la terminologie de "type" à ces fruits (Cornet 2001, Baudoin et al. 2002).

Actuellement, pour des besoins économiques, *E. guineensis* a une distribution pantropicale et fait l'objet d'importants travaux d'amélioration génétique, hybridation et clonage (Comte 1991, Cornet 2001, Baudoin et al. 2002). Ces opérations sont nécessaires pour l'exploitation et la valorisation de son potentiel économique, car le palmier à huile originel met en moyenne une trentaine d'année pour atteindre sa maturité physiologique, dont la manifestation principale est la floraison qui induit la fructification (Comte 1991, Cunningham 1997).

Les caractères morphologiques des différents morphotypes n'étant pas tranchés au niveau des organes végétatifs, seules les propriétés liées aux fruits permettent une classification (Chevallier 1910, Cornet 2001, Baudoin et al. 2002). Celle-ci est axée sur l'épaisseur de l'endocarpe (coque)

d'une part, et la couleur des fruits d'autre part. En fonction de l'épaisseur de l'endocarpe on distingue:

- le dura, avec un endocarpe de 2,5 à 7 mm d'épaisseur est le plus répandu en milieu naturel et paysan. De la masse du fruit, l'endocarpe représente environ 60%;
- le tenera, avec un endocarpe dont l'épaisseur est inférieur ou égal à 2,5 mm. Il représente environ 13% de la masse total du fruit. Ce morphotype constitue la majorité des peuplements des plantations industrielles;
- le pisifera, dépourvu d'endocarpe sclérifié est presque sans grande valeur.

La classification basée sur la couleur des fruits n'est pas en rapport avec la spécificité des morphotypes aux fruits tenera, dura ou pisifera. La variabilité de la couleur des fruits (tableau 1), notée du développement morphologique à la maturité physiologique conduit à distinguer:

- les fruits nigrescens (appendice électronique, photographies D-I)
- les fruits virescens (appendice électronique, photographie A)
- les fruits albescens: albo-nigrescens et albo-virescens (appendice électronique, photographies B & C).

La revue de la littérature des travaux d'ethnobotanique où intervient *E. guineensis*, ne fait aucune mention distinctive sur les différents types de fruits (nigrescens, virescens et albescens; albo-virescens et albo-nigrescens) dans les usages. Cette étude, orientée sur les habitudes et les mœurs des populations congolaises à l'égard des morphotypes de *E. guineensis*, souligne des comportements spécifiques liés à la couleur du fruit. De tous les types de fruits distingués suivant la couleur, ce sont les virescens et les albo-virescens qui focalisent principalement l'intérêt de cette étude et dans la moindre mesure les albo-nigrescens.

Les objectifs poursuivis par cette étude se basent essentiellement sur trois aspects se définissant comme suit:

- circonscrire le territoire géographique de distribution des morphotypes de *E. guineensis* aux fruits virescens et albo-virescens
- suivre et mettre en exergue les mœurs liées aux fruits virescens et albo-virescens
- mettre en relief les tendances sur le devenir des populations des morphotypes de *E. guineensis* aux fruits virescens et albo-virescens.

MATERIEL ET MÉTHODE

Cette étude ethnobotanique s'est déroulée dans la période allant de mars 2002 à avril 2004. Elle couvre tout le territoire congolais, où la présence des morphotypes aux fruits vires-

Tableau 1 Caractérisation des différents types de fruits d'*Elaeis guineensis* en fonction du stade de développement
Variation de la couleur des différents types de fruits d'*Elaeis guineensis* de la fructification à la maturité.

Type de fruits		Couleur du fruit		Références
		Avant maturité	A maturité	
Nigrescens		Noire à reflets violets	Jaune orangé et noir à l'extrémité supérieure	Chevallier (1910)
Virescens		Verte	Jaune orangé clair et vert à l'extrémité supérieure	Beccari (1914)
Albescens	Albo-nigrescens	Noire	Jaune pâle et noire à l'extrémité supérieure	Cornet (2001)
	Albo-virescens	Verte	Jaune pâle et verte à l'extrémité supérieure	Baudoin et al. (2002)

cens et albo-virescens est avérée (fig. 1). Les enquêtes se sont déroulées uniquement dans les localités où la présence d'un ou de plusieurs morphotypes d'*Elaeis guineensis* était avérée. A défaut de preuves, les informations sont systématiquement écartées. Elles concernent les groupes ethniques/linguistiques des villages des localités administratives suivantes:

Région de la Bouenza

- Districts de Madingou et Kayes: groupe ethnique/linguistique Kaamba
- District de Loudima: groupes ethniques/linguistiques Kaamba et Kougni
- District de Mfouati: groupes ethniques/linguistiques Kaamba et Doondo
- District de Mouyondzi: groupe ethnique/linguistique Beembe
- District de Boko-Songho: groupe ethnique/linguistique Doondo

- District de Yamba: groupe ethnique/linguistique: Minkengué

Région du Niari

- District de Kibangou: groupe ethnique/linguistique Kougni

Région du Pool

- District de Boko: groupe ethnique/linguistique Koongo

Région du Kouilou

- District de Tsiamba-Nzassi: groupe ethnique/linguistique Mvili

Région de la Lékoumou

- District de Sibiti: groupe ethnique/linguistique Yaka

Région de la Cuvette

- District d'Oyo: groupe ethnique/linguistique Mbochi
- District d'Owando: groupe ethnique/linguistique Kouyou.

La connaissance traditionnelle et l'exploitation de la biodiversité sont généralement des données relatives et sou-



Figure 1 - Localisation des sites d'enquête en République du Congo.

Tableau 2 - Données ethnobotaniques et phytogéographiques sur les morphotypes aux fruits virescens et albo-virescens d'*Elaeis guineensis*.

Maux et usages associés aux groupes ethniques/linguistiques en fonction de la répartition géographique des morphotypes aux fruits virescens et albo-virescens; *: usages tenant de la spécificité des fruits virescens et albo-virescens.

District phytogéographique	Groupes ethniques	Interdits	Usages (*)
Kouilou	Mvili	-	Médicinal, magicothérapie
Chaillu	Yaka	-	Magicothérapie, pratiques ésotériques et exotériques
Niari	Kaamba Kougni Minkengué Beembe	Gastrite, lèpre, stérilité masculine	Alimentaire, médicinal, pratiques ésotériques et exotériques
Cataractes	Doondo Koongo	Lèpre, furonculose	
Alima	Mbochi Kouyou	Lèpre	Alimentaire, Médicinal

vent claniques voire communautaires, l'échantillon d'étude ne peut être une donnée quantitative au sens statistique du terme, mais plutôt qualitative. Pour cette raison, la taille de l'échantillon n'est pas une donnée majeure par rapport aux sources et à la pertinence de l'information. L'étude ne se basant pas sur une évaluation comparative des connaissances entre les genres, aucune différence n'est marquée pendant le recueil de l'information. Notre échantillon d'informateurs dont l'âge varie de 15 à 70 ans est basé sur la mixité du genre et se compose des jeunes adolescents, d'adultes et de vieux. Le nombre d'informateurs par village où par localité n'est pas exprimé en fonction du nombre de résident, mais plutôt en nombre d'individus ayant identifié la ressource et possesseurs de la connaissance sur les vertus associées. C'est ainsi que notre échantillon d'informateurs regroupe 351 personnes dont 143 femmes.

Les morphotypes d'*E. guineensis* aux fruits virescens et albo-virescens reconnus et identifiés, nos enquêtes se sont cristallisées sur: les entretiens personnalisés et les focus group impliquant les deux genres (Martin 1995); et le suivi des produits sur le marché des localités d'enquête, afin de noter le comportement des ménagères. Ces entretiens sont semi directifs et se basent sur un guide d'entretien à questions ouvertes, ce qui évite d'influencer la réponse des informateurs (Martin 1995). La démarche ethnobotanique consiste à identifier la ressource, connaître les vertus qui y sont associées ou qui y ont été associées. Enfin, elle est ponctuée par la reconnaissance de la ressource dans les vergers privés et emplacement des anciens villages.

Outre les entretiens et les focus group, nous notons le groupe ethnique et l'origine, autochtone ou allochtone, de nos informateurs.

RÉSULTATS

Cette étude donne des informations sur la distribution de la ressource sur le territoire congolais d'une part, et d'autre part, elle nous renseigne sur les interdits et les usages liés aux fruits virescens et albo-virescens des morphotypes d'*E. guineensis* (tableau 2).

Distribution phytogéographique

L'inventaire de la ressource a montré que les morphotypes de palmiers incriminés ont été recensés dans cinq districts sur onze que compte le territoire congolais (tableau 2). Il s'agit des districts phytogéographiques du Kouilou, du Chaillu, du Niari, des Cataractes et de l'Alima (Kimpouni et al. 1992). Excepté le Chaillu qui est forestier, les morphotypes aux fruits virescens et albo-virescens de *E. guineensis* se retrouvent en zone de savane. En fonction de cette répartition, des spécificités d'usages et de mœurs sont relevées pour les différents types de fruits. Dans les districts du Kouilou et du Chaillu en dépit des usages recensés, aucun interdit n'est relevé.

Aspects ethnobotaniques et phytothérapies

L'aspect ethnobotanique recense quatre interdits liés principalement à la consommation des fruits virescens et albo-virescens, et dans la moindre mesure ceux du type albo-nigrescens (tableau 2). Des quatre interdits connus, la lèpre est la plus commune avec un rapport communautaire de huit sur dix groupes ethniques/linguistiques enquêtés, d'une part, et d'autre part trois districts sur les cinq hébergeant les morphotypes incriminés. Outre ces interdits, les propriétés magicothérapeutiques associées aux fruits virescens et albo-virescens sont largement exploitées au sein des communautés ethniques/linguistiques enquêtées.

Pour soulager leurs maux, certaines populations ont recours, de manière systématique, à l'usage des différentes parties du fruit virescens ou albo-virescens. Ces sociétés, aux pratiques claniques ou non, utilisent les différents fruits d'*E. guineensis* pour soigner de nombreux maux. Certaines recettes proviennent de la médecine traditionnelle classique, d'autres sont plutôt associées à des rituels de magicothérapie (essentiellement ésotériques, parfois exotériques). Au cours de cette étude, les cas observés ou notés en fonction des groupes ethniques/linguistiques sont les suivants:

- dans le groupe Mbochi, l'huile des fruits est utilisée pour les soins des otites, les noix pour les brûlures occasionnées par la foudre ou tout autre symptôme en relation avec le foudroiement. Elle sert encore au traitement

d'une sorte de dermatose de type zona, communément nommée 'muandza' et liée au mauvais sort;

- les groupes Kouyou, Mbeembe et Mvili trouvent une source non négligeable de médicaments dans les fruits virescens et albo-virescens;
- chez les Kougni, ces fruits sont impliqués dans le traitement de plusieurs maux des voies respiratoires;
- les populations du Chaillu utilisent spécifiquement les huiles des fruits virescens et albo-virescens pour les pratiques magicothérapeutiques et ésotériques;
- Enfin, toutes ces communautés ethniques/linguistiques utilisent les fruits du morphotype tenera, et principalement le noyau pour soulager leurs maux. Qu'importe qu'il soit nigrescens, virescens ou albescens (albo-virescens ou albo-nigrescens). En relation avec le traitement appliqué aux individus des différents morphotypes, les noyaux dans ce cas proviennent généralement des fruits nigrescens et albo-nigrescens. La présence de ce produit sur les étals des commerçants, plus ou moins, spécialisés dans la vente des produits de la médecine traditionnelle dans les principales villes, traduit la dimension lucrative qui y est associée.

Relief sociolinguistique

La spécificité linguistique permet de déceler que ce palmier est 'atypique'. Différent d'*E. guineensis* aux fruits nigrescens ou albo-nigrescens, son nom est formé soit d'un préfixe ou soit d'un suffixe, accompagnant le nom du palmier commun (ba et ibia); le cas échéant son appellation est particularisée. C'est ainsi que nous avons des noms comme 'mu mpeti', 'matundubula' et 'onuna'. Suivant les zones et les groupes ethniques/linguistiques, le palmier (*E. guineensis*) portant les fruits virescens ou albo-virescens est appelé:

- 'ba dia nkabi, matunda ba' (dialectes Kaamba et Doondo);
- 'mbati' (dialecte Doondo);
- 'mutundu ba, matunda ba' (dialecte Kougni);
- 'ba dia matundubula, matundubula' (dialecte Minkengué);
- 'ibia l'onuna, onuna' (dialecte Kouyou);
- 'ibia onona' (dialecte Mbochi);
- 'mbâ za malahou, mbâ za mintuskila' (dialecte Beembe);
- 'ntuta' (dialecte Koongo);
- 'mu mpeti' (dialecte Mvili);
- 'misombo' (dialecte Yaka).

Ces fruits qui subissent souvent la prédation des antilopes (diverses espèces de céphalophes), sont incriminés dans la transmission de la lèpre chez l'homme. Ce lien, avéré ou non, suffit pour justifier le nom vernaculaire de 'ba dia nkabi', littéralement traduit par 'le palmier de l'antilope'. Quant aux autres appellations, elles sont relatives à la coloration verte des fruits juvéniles. C'est ainsi, nous avons 'ibia onona' ou palmier à noix vertes. Enfin, 'matunda ba' et 'ba dia matundubula' seraient composées et associées au développement des fruits d'*Aframomum* spp. (verdâtre à l'état juvénile et rougeâtre à maturité physiologique);

Toutefois, il est intéressant de constater que dans le groupe ethnique/linguistique Doondo, des différences très précises, suivant les localités, sont notées dans la nomination

et les usages des palmiers aux fruits virescens et albo-virescens. Les différences suivantes sont inscrites:

- 'mbati' pour désigner les fruits virescens (non comestibles et à usage artisanal);
- 'matunda ba' pour les fruits albo-virescens (comestible, mais interdit à certaines personnes à cause de la furonculose dont ils seraient à l'origine).

Mœurs et empirisme des populations

Les fruits albo-nigrescens, comestibles, et ne comportant pas le même interdit alimentaire que les fruits albo-virescens, seraient à l'origine de la coloration noirâtre des sauces. Par contre, selon les informateurs, les sauces à base de fruits virescens et/ou albo-virescens seraient très impliquées dans l'origine des poussées gastriques (connues sous le nom vernaculaire de 'kikendola' en Kaamba) et les affections lépreuses, et provoqueraient également la stérilité masculine. Les enquêtes ont porté sur plusieurs groupes ethniques/linguistiques, dont la perception des fruits virescens et albo-virescens est différente. Les spécificités relevées sont:

- tenant compte de la dualité antilope (y compris les grands céphalophes) et lèpre au sein des groupes ethniques/linguistiques l'observant, la consommation de ces fruits est interdite à toutes les personnes ayant contracté la lèpre. Il y va de soit que la consommation de la viande d'antilope leur soit également prohibée. A propos de l'interdiction de la consommation des fruits virescens et albo-virescens, et de la viande d'antilope y compris de grands céphalophes, plusieurs raisons y concourent outre celle liée à la lèpre. Les hémorroïdes et la furonculose sont, entre autres, les causes les plus citées;
- chez les Minkengué, les fruits virescens et albo-virescens seraient responsables de la stérilité masculine. Pour cette raison, ils ne peuvent être consommés par les adolescents, les jeunes adultes et les hommes qui n'ont pas d'enfants. Ainsi, la récolte des fruits virescens et albo-virescens est exclusivement réservée aux hommes ayant des enfants. Quant à la consommation des sauces à base de ces fruits, seuls les hommes représentant la caste sociale du village y à droit. Cette catégorie de personnes reçoit gratuitement ces fruits et ce geste traduit ou mieux encore symbolise la valeur sociale qui y est attachée.

Valeur socio-économique et patrimoine génétique

La sauce à base de noix de palme étant très prisée dans la région, le commerce de ce produit n'est pas négligeable, sur les marchés locaux, mais pour des raisons toutes évidentes, les ménagères, appliquant les tabous alimentaires en vigueur dans leur groupe ethnique/linguistique, évitent systématiquement d'acheter les fruits virescens et albo-virescens. Ce constat est aussi vérifié dans les foyers pourvoyeurs du marché en noix de palme. Il se manifeste par une séparation stricte des fruits nigrescens des virescens et albo-virescens. Cette pratique induit de facto une mévente de ces derniers, sur les marchés des différentes contrées où la plante est présente. Dans l'ensemble des territoires où les différents morphotypes sont représentés, l'information recueillie montre que l'utilisation alimentaire des fruits virescens et albo-virescens n'est pas aussi prononcée qu'elle l'est pour les fruits nigrescens. Seuls

quelques individus, dans presque tous les groupes ethniques/linguistiques, les inscrivent au chapitre alimentaire comme produit frais. Cependant, la consommation des produits dérivés de ces fruits, notamment l'huile de palme dans ce cas précis, ne suscite aucune interrogation dans tous les groupes ethniques/linguistiques.

Eu égard aux questions touchant à la valeur socioculturelle notée, dans certaines contrées, et la mévente que connaît le produit, les tendances dans le processus d'érosion génétique n'accusent pas le même degré. Le constat découlant de l'enquête dénote que:

- dans les régions où le lien avec la lèpre est très fort, une destruction presque systématique des individus aux fruits virescens et albo-virescens est observée. Les propriétaires des vergers ne laissent presque pas ces morphotypes se développer. Très souvent, et dans les proportions de 2/3, les individus sont abattus dès la première fructification;
- par contre, dans les sociétés où une valeur sociale est relevée, la pression anthropique destructrice est presque nulle. C'est dans ces zones qu'est enregistrée une assez bonne représentativité des morphotypes aux fruits virescens et albo-virescens dans les vergers. Cette tendance est prononcée chez les Beembe et les Minkengué.

DISCUSSIONS ET COMMENTAIRES

Les résultats de cette étude conduisent à examiner les questions mises en exergue par nos objectifs dans l'optique de la dynamique de colonisation des territoires géographiques, de la conservation de la diversité biologique et enfin la confirmation et l'infirmité des vertus associées aux fruits virescens et albo-virescens des morphotypes du palmier à huile.

Occupation spatiale

E. guineensis est une essence écologiquement exigeante en lumière, en ensoleillement et en température, pour un optimum de croissance et de rendement (Cornet 2001, White 1986). Qualifiée d'héliophile obligatoire par Cornet (2001), ses besoins en ensoleillement sont de l'ordre de 1800 heures/an et cet élément devient un facteur limitant autour de 1500 heures/an. La température de prédilection pour cette espèce se situe entre 24 et 26°C, avec des écarts autour de la moyenne ne dépassant 10°C; enfin, la lumière doit être intense et continue. En rapport avec les habitats, la savane seule est à mesure de satisfaire ces exigences écologiques. Elle serait le milieu indiqué pour *Elaeis guineensis*. La présence de *E. guineensis* étant liée à l'histoire des hommes et de leurs besoins, cette espèce est actuellement présente sur tout le territoire, zone forestière comprise. Nonobstant les critères écologiques naturels, l'introduction d'*E. guineensis* en zone forestière remonte aux années 1925–1930 (Vennetier 1977). La mise en place des palmeraies dans les localités de Mokeko et d'Itoumbi (dans le massif forestier du Nord Congo) et, de Sibiti et de Komono (dans le massif forestier du Chaillu) a nécessité une coupe à blanc de la forêt, pour la satisfaction des exigences écologiques de la plante.

La distribution phytogéographique des morphotypes aux fruits virescens et albo-virescens au Congo, montre qu'ils sont principalement installés dans les territoires où domine

la savane (Descoings 1975). En dépit de cette pratique culturelle, les informations relatives à l'existence de ces morphotypes dans les zones forestières comme le Chaillu, voire le Mayombe, tendent à prouver qu'elle serait due au fait que la gestion, tout comme leur introduction, est l'œuvre des populations autochtones. Le caractère indigène du palmier à huile n'étant pas prouvé formellement en zones forestières, ces raisons sont plus que plausibles pour justifier la présence ou l'absence de certains morphotypes au sein de ces écosystèmes.

Cet argumentaire soutenant que *Elaeis guineensis* n'est pas sauvage en zones forestières, les morphotypes aux fruits virescens et albo-virescens auraient été introduits concomitamment avec le morphotype aux fruits nigrescens, sans signe particulier lors de la mise en place des palmeraies. Le cas échéant, les causes de l'extension de leur aire peuvent être recherchées dans la curiosité qu'ils suscitent ou dans les vertus y étant associées. Cette raison peut légitimer la dualité qui, d'une part, approuve le fait qu'ils ne puissent pas avoir une appellation particulière dans les différents dialectes en usage dans le Chaillu ou en zones forestières, et, d'autre part, qu'il n'y soit pas associé des interdits connus. Comme le souligne Martin (1995), une analyse linguistique des différentes appellations est nécessaire pour montrer les emprunts lexicaux et ressortir les usages et les interdits intrinsèques à chaque groupe ethnique/linguistique.

Maintien des populations in situ

Les caractères morphologiques et biométriques ne permettent pas de distinguer les plantes aux fruits virescens et albo-virescens des autres (nigrescens et albo-nigrescens), et les tentatives descriptives, appuyées par la connaissance traditionnelle, qui sont relevées sur le terrain confirme ce fait. Il est donc évident que les populations vivant dans les zones où la mentalité ou mieux le regard envers les morphotypes incriminés n'a guère évolué les détruisent dès la première fructification. N'eut été cette difficulté d'identification, l'éradication de ces morphotypes serait encore plus accentuée. La magicothérapie, la médecine traditionnelle et les pratiques ésotériques ne requièrent pas de grandes quantités de produits, d'où le maintien in situ d'une population limitée à quelques individus des morphotypes aux fruits virescens et albo-virescens. Cette attitude est plus prononcée dans les sociétés où le lien avec la lèpre est très fort.

Outre la valeur socioculturelle soulignée au sein des sociétés traditionnelles, l'élimination des morphotypes aux fruits virescens et albo-virescens est accentuée par l'installation des palmeraies 'monovariétales', à base du morphotype tenera aux fruits nigrescens. En milieu paysan où le morphotype dura, tous les fruits confondus, est le plus commun, on mentionne son remplacement par le morphotype tenera aux fruits nigrescens. Cette attitude est liée aux nombreux avantages issus de l'amélioration génétique d'*E. guineensis* (Comte 1991, Cornet 2001). Néanmoins, cette amélioration se fait au détriment de la rusticité des individus et de la variabilité génétique.

Les données de la composition chimique des fruits et les analyses de l'huile de palme ont montré que ces produits sont respectivement très riches en substances extractibles

non azotés d'une part, et d'autre part en acides gras (insaturé et saturé) et en caroténoïdes, notamment en vitamine A (Cornet 2001). La dimension psychologique qui entoure les fruits virescens et albo-virescens couplée aux vertus thérapeutiques avérées d'*E. guineensis*, en médecine traditionnelle, sont des signaux guère surprenants de ces produits à occuper une place de choix dans la préparation des recettes phytothérapeutiques (Bouquet 1969, Adjanohoun et al. 1988, Diafouka & Lejoly 1998).

Considérations empiriques

Si les sauces grasses sont parfois et souvent responsables des poussées gastriques, les substances contenues dans le fruit et l'huile ne peuvent être tenues comme agents favorisant les affections lépreuses et la stérilité masculine. En d'autres termes, ces substances sont incapables d'induire la virulence du bacille responsable de la lèpre et de la furonculose, tout comme elles n'ont pas un pouvoir physiologique susceptible de perturber la spermatogenèse ou encore les fonctions liées à la virilité masculine. Ces griefs attribués aux fruits virescens et albo-virescens et reconnus empiriquement sont non fondés. En effet, la consommation d'huile de palme où des sauces à base des fruits virescens ou albo-virescens, par les individus de tout âge et des deux sexes, n'affecte nullement leur santé. Toutefois, les fruits virescens et albo-virescens, pour ces sociétés traditionnelles, ont une valeur sociale indéniable dans l'éducation des jeunes.

Dans leur travail sur les plantes utiles du Gabon, Raponda-Walker & Sillans (1961) soulignent l'existence des morphotypes aux fruits virescens et les usages multiples associés à *Elaeis guineensis*. L'intérêt de cette plante résulte de la diversité des produits qui sont tirés et de leur domaine d'utilisation. Les aspects couverts vont de l'usage traditionnel des sociétés africaines (alimentaires, cosmétologiques, phytothérapeutiques et artisanaux) aux besoins technologiques et de développement industriel des biodiesels, des détergents et des lubrifiants (Prota 2009). En dépit des différences d'appellation notées au sein des groupes ethniques/linguistiques gabonais, distinguant les fruits virescens des nigrescens, aucune spécificité ethnobotanique en rapport avec ces deux types de fruits n'est évoquée (Raponda-Walker & Sillans 1961). Au stade actuel des connaissances sur les moeurs liées aux fruits virescens et albo-virescens d'*Elaeis guineensis*, les pratiques décrites dans cette étude sont une authentification des sociétés traditionnelles Congolaises.

CONCLUSION

A tort ou à raison, le procès autour des fruits virescens et albo-virescens n'est pas fondé et le non maintien in situ des populations de ces morphotypes est un signe d'éradication, dans un futur très proche, de ce potentiel génétique. Cette tendance qui est très prononcée dans les zones où leur lien avec la lèpre serait avéré, a inculqué des comportements négatifs à leur égard. L'amélioration génétique d'*E. guineensis* dont les corollaires sont la précocité reproductrice et l'accroissement du rendement, amplifie le rythme de déclin

des morphotypes aux fruits virescens et albo-virescens en particulier.

Des efforts sont à consentir dans la persuasion des populations à garantir l'existence et la viabilité des morphotypes aux fruits virescens et albo-virescens. Leur disparition, à plus ou moins court terme, ne doit pas être vécue comme un gain au profit de l'amélioration du rendement, mais plutôt une perte 'irréversible' du patrimoine génétique et culturel. Les conséquences de celle-ci se traduisent dans les implications en matière de recherches d'amélioration génétique et de lutte contre les maladies. En effet, l'engouement que les populations manifestent actuellement pour le morphotype tenera aux fruits nigrescens peut s'évanouir en un laps de temps très court, dans le cas où une maladie décimerait les individus de ce morphotype. Il est donc souhaitable que soit mise en culture une population hétérogène des morphotypes de palmiers à huile, afin de servir de réservoir de gènes.

MATERIEL SUPPLEMENTAIRE

Le matériel supplémentaire est disponible au format pdf sur le site du matériel supplémentaire des publications du Jardin botanique national de Belgique (<http://www.nbgpublisher.be> > SBB50 > dossier 523) et consiste en des photographies des fruits virescens, albo-virescens et nigrescens d'*Elaeis guineensis*.

REMERCIEMENTS

Nous tenons à remercier toutes les personnes (informateurs, guides, traducteurs et autorités locales) qui, en dépit de leurs multiples occupations, ont loyalement collaboré à la réalisation de ce travail. Cette étude est le fruit de votre accueil sans faille et du temps investi. L'équipe loue votre disponibilité permanente et votre sollicitude qui est sans borne. A tous ceux qui ont aidé à l'amélioration du manuscrit, notamment Natacha Beau, du Jardin Botanique de Meise, nous disons grand merci.

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- Manuscript received 21 Sep. 2010; accepted in revised version 26 Sep. 2011.
- Communicating Editor: Elmar Robbrecht.



East African plant use – differences in plant use between nomadic and agricultural societies

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Background and aims – This paper compares the plant use of originally nomadic (Sekenani and Loita Maasai in Southern Kenya, Samburu of the Mt. Nyiru area in Northern Kenya) and agricultural (Kikuyu in central Kenya, Oromo in Southern Ethiopia) societies.

Methods – The lead hypothesis was that traditional nomadic societies would have larger plant knowledge than their more westernized counterparts, and that both would have more knowledge than agricultural societies. In addition, it was assumed that nomadic societies would know more about traditional veterinary medicine than their sedentary counterparts. These hypotheses were tested using open ended interviews.

Key results – The change from a nomadic to a more sedentary lifestyle, has affected the Samburu to a much lesser extent and so far did not lead to a major loss of traditional plant knowledge. In case of the Sekenani Maasai, the recent change from a nomadic to a more sedentary lifestyle has led to a loss of traditional plant knowledge, when compared to other Maasai communities. The Kikuyu, occupying one of the most densely populated areas in Kenya, maintained a surprisingly high knowledge of plants used for veterinary purposes, in the treatment of malaria and sexually transmitted diseases, while other traditional knowledge has mostly disappeared. Plant use amongst the Oromo has almost disappeared due to close access to Western medicine.

Conclusions – Knowledge of plants for veterinary purposes was however, unexpectedly, highest amongst the Kikuyu. This traces back to the fact that western veterinary medicine, both sponsored by governments and NGOs, is best developed in major livestock areas, rather than in areas where agriculturalists might have just one cow in their backyard.

Key words – Samburu, Maasai, Kikuyu, Oromo, Kenya, Ethiopia, ethnobotany, plant use, traditional knowledge, utilization.

INTRODUCTION

Traditional plant use is of tremendous importance in many societies, including most rural African communities. This knowledge is however, rapidly dwindling due to changes towards a more Western lifestyle, and the influence of modern tourism. Nomadic societies are often amongst the more traditional groups in any given region, since they tend to occupy more remote areas, and their contact to mainstream society tends to be more limited. Since the early 1990s we studied the vegetation composition and regeneration processes of mountain forests in Eastern Africa in a large transect stretching from Southern Kenya to Northern Ethiopia. This work, involving over 1,000 plots with complete vegetation inventory, served as ideal base for the comparison of the plant use of communities in the region (Bussmann 1994, 1997, 2002, Bussmann & Beek 1995, Bytebier & Bussmann 2000).

Plants have been an integral part of life in many indigenous communities, and Africa is no exception (Sindiga et al. 1995a, 1995b, Barrow 1996). Apart from providing building materials, fodder, weapons and other commodities, plants are especially important as traditional medicines. Western influences have however led to an accelerating decline of this tradition. Most knowledge is still transferred entirely orally in many communities (Fratkin 1996). Western style health-care supplied by the government has expanded in the last decades, but it is still often not readily available and many regions remain completely underserved. Subsequently, most communities still use herbal remedies as readily and cheaply available alternative. The creation of game reserves has led to restrictions in the movements of nomadic communities like the Maasai and Samburu, and has restricted their grazing grounds (Homewood & Rodgers 1991, Akama 1999, Fratkin & Mearns 2003, Lamprey & Reid 2004, Kiringe 2005). When

starting to study plant use in the Kikuyu, Maasai, Samburu and Oromo societies in the early 2000s, we hypothesized that the most traditional nomadic communities would have more in-depth plant knowledge in comparison to communities e.g. living closer to population centers. In addition, we believed that agricultural communities, often living in the most densely populated areas of the region, in closer proximity to larger cities, would use fewer plants for their medical needs, and in addition would not maintain a broad knowledge in veterinary medicine. Some of the ethnobotanical results have been reported elsewhere (Bussmann 2006, Bussmann et al. 2006, Njoroge et al. 2004, Njoroge & Bussmann 2006a, 2006b, 2006c, 2007, 2009). The present paper attempts a comparison of all communities studied, based on malaria, sexually transmitted diseases and veterinary medicine, which appeared to be of special relevance in all the societies involved.

Malaria

Malaria is still a major global public health problem in most tropical countries. It is thought that malaria is by far the most serious tropical disease causing one to two million deaths per year, and it plays a major role in the high mortality seen in infants and children (El Kamali & El Kijalifa 1997, Milliken 1997). It is also responsible for miscarriages, premature deliveries, growth retardation, low birth weight and anemia (Connally et al. 1996, Geissler et al. 1998, Minakawa et al. 2002, Hay et al. 2003). The World Health Organization (WHO) has estimated that about 2 billion people in over 100 countries are exposed to malaria, with 247 million cases in 2006 alone, and half of the world's population is potentially exposed to the disease, and Africa being one of the main centers of the disease (WHO 2009). The worsening global economic situation makes it difficult to expand modern health services, hence effective low-cost delivery medical system is urgently needed (El Kamali & El Kijalifa 1997). In Kenya alone malaria is responsible for 30–50% out patient treatments, 19% admissions and accounts for 8–10 million treatments per year (Ochola 2003). Factors that make malaria treatment unaffordable include rising costs of non-chloroquine drugs, high poverty levels as well high prices of insecticide treated nets (Guyatt et al. 2002).

Veterinary plant use

Livestock is an important part of livelihood and culture in Sub-Saharan Africa especially (Ghirotti 1996). Livestock diseases play a major role in African countries in particular because unlike in other continents all five most important livestock diseases occur here (van Veen 1996), with anaplasmosis and theileriosis being endemic in sub-humid Africa (Msellati & Tachers 1991). It has been established that animal diseases are a major constraint to livestock production in Kenya (Delehanty 1996, Keengwe & Bekalo 1996, Githiori 2004). Prevention and control of animal diseases therefore have been of critical concern in Kenya like in other African countries. Although the livestock industry in Kenya contributes only about 10% to the GDP there is potential for improved production if appropriate measures are taken in disease control. Just like in human health care the cost of conventional veterinary medicines has escalated in the recent past and has become

unaffordable to most stock raisers in most African countries, causing smallholder farmers to turn to low cost alternatives. In Zimbabwe for example, ethnoveterinary medicine is gaining recognition at the expense of conventional drugs especially because of its greater accessibility, lower costs and apparent effectiveness (Mwale et al. 2005). The use of traditional plants for management of diseases both in animals and humans is not haphazard. In Kenya for example, at Kaloleni division, a correspondence has been established between ethnoveterinary data and laboratory serological data regarding theileriosis in calves (Delehanty 1996). Among the Samburu and Turkana research has shown that 35 diseases, including streptothricosis, mange, cough and diarrhoea are treatable using local remedies (Wanyama 1997). Some of these discoveries have begun to generate research in the area of ethnoveterinary in the eastern African region (Delehanty 1996, Heffernan et al. 1996, Wanyama 1997, Githiori et al. 2002, Waihenya et al. 2002a, 2002b, Githiori et al. 2003, Tabuti et al. 2003, Githiori 2004). Such research in Kenya however, is limited and has focused on ethnoveterinary practices among pastoral and farming communities in marginal areas. Farming communities in high potential areas such as Central Kenya, where many farmers have relied on cash crops such as coffee, have now turned to alternative means of livelihood such as cattle keeping due to reduced prices for their crops. Although some of this information has been documented in some parts of Kenya, it has been shown that knowledge on ethnoveterinary medicine varies from region to region as well as within and among communities (Matekaire & Bwakura 2004).

Sexually transmitted diseases

In African societies, sexually transmitted infections have been managed with plant materials for centuries. In Zimbabwe for example, sexually transmitted diseases (STDs) such as gonorrhea, genital herpes, syphilis and hepatitis have been managed with various plant extracts by traditional healers for a long time (Kambizi & Afolayan 2001). In South Africa, the general behavior is that patients with STDs go to the traditional healers as there is general believe that traditional medicines are more effective than western medicines in dealing with these diseases (Tshikalange et al. 2005). Plant used by such healers need documentation and consequent screening for their efficacy. In the Central Province of Kenya alone, there are about 240,000 individuals infected with HIV, while the prevalence rates are estimated at 13%. Although there has been an increase in the use of herbal preparations in managing various illnesses in Kenya, there are no systematic studies to document the plants used in Central Kenya for management of STDs and reproductive health. Such documentation is essential for targeting plants for screening against bacteria, viruses, fungi as well as parasites responsible for sexually transmitted diseases.

STUDY AREA

The presented study was carried out in a vast area stretching from the Northern Slopes of Kilimanjaro in Southern Kenya, northwards to Northern Bale in southern Ethiopia (fig. 1)

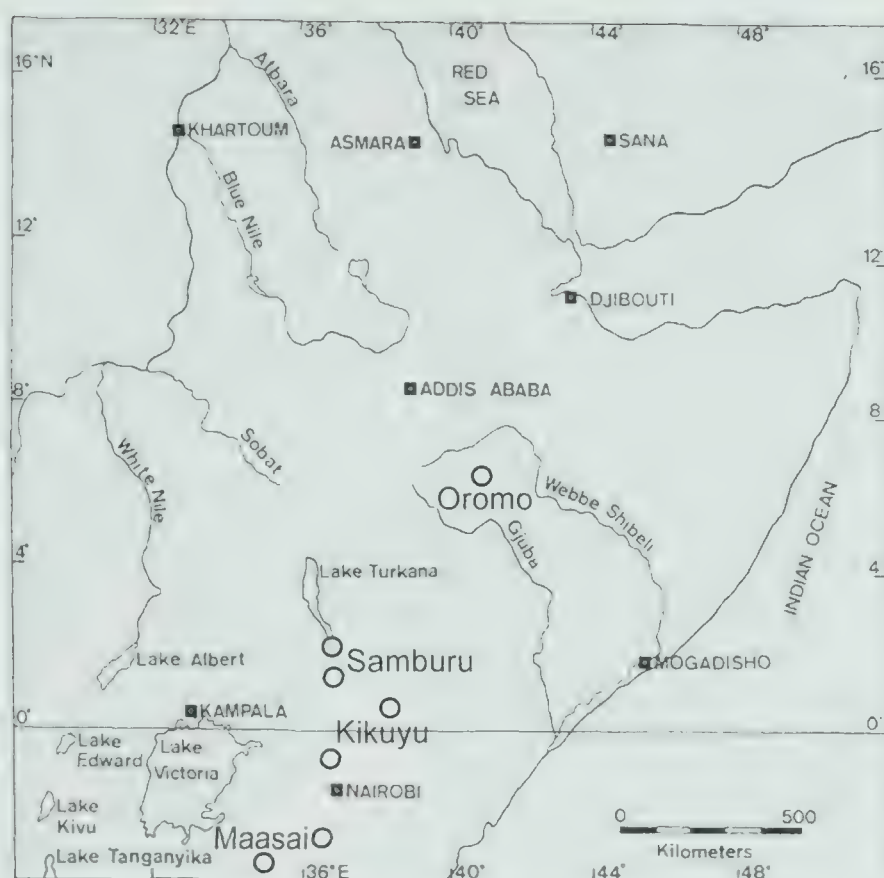


Figure 1 – Study area. Research areas as black circles.

This region has in parts high population density and large concentration of forests, which are facing intense pressure due to over-utilization and hence medicinal plants may be disappearing before their uses are documented. As example, formerly extensive areas of the Ethiopian highlands were covered with forests. The National Atlas of Ethiopia (Fanta 1981) estimates that more than 30% of the country or about 370,000 km² have been forested in historic times. Today, even a forest cover of 10% is probably an overestimate. Large parts of these remaining forests are heavily impacted by agriculture, logging and exploitation for firewood. The situation is even direr in Kenya.

The Northern part of the study region in Kenya consists of vast alluvial inland plains, inclining from altitudes of about 1,200 m to the North of Mt. Kenya to barely 400 m around Lake Turkana. On the Southwest, a chain of mountains consisting of old crystalline Precambrian basement rocks, mainly extremely durable gneisses and granites borders the plains. For this reason, the steep Ndoto and Nyiru Ranges, reaching up to 2,752 m, were left standing during the different erosion cycles influencing the region. Next to these, a series of Quaternary volcanic peaks, like Mt. Kulal (2,285 m), Mt. Marsabit (1,707 m) and the Huri Hills (1,479 m), overshadowed by the Bale Chain in southern Ethiopia (4,200 m), the large peaks of the Aberdares and Mt. Kenya in Central Kenya, dominate the landscape. The soils of the plains consist mainly of Vertisols, Regosols, Lithosols and Cambisols. The mountain slopes are covered with humic Nitisols and Acrisols in case of the basement formations and the lower volcanic areas, and deep humic Andosols above about 2,700 m (Mäkel 1986, Mäkel & Schultka 1988, Mäkel & Walter 1983, Schmitt 1991).

According to the climatological classification of Jätzold (1977, 1981), the plains of northern Kenya and southern Ethiopia are part of the hot, arid tropical climate, with two short sub-humid seasons. Mean monthly temperatures range

from 20–26°C in the plains, to 17–19°C in the mountains (Gatab, 1,657 m). The average annual rainfall can be as low as 100–150 mm in the Hedad plain and Chalbi desert, rising to 500 mm in the valleys of the Nyiru and Ndoto mountains. In the mountain forest zone, a rainfall of about 2,500 mm can be reached. The main rainfall is concentrated in two wet seasons, from March to May and from October to December (Kenya Meteorological Department 1974/1984).

Vegetation

Most of the study areas are covered with evergreen montane forest, and the vegetation is by now well studied. These forests owe their existence to the humidity received from mist condensation and frequent cloud formation in the peak areas. Neumann (1898) after visiting the southern Turkana Region wrote: “The western face of Nyiru is topped with dark forests, and here and there hang waterfalls, filled with the outpourings of the heavy clouds which often cap the summit.” Due to their enormous importance as water catchments most mountain areas are gazetted as forest reserves. The extent of these reserves, however, does not really reflect the amount of land actually covered with forest. The Mt. Nyiru forest reserve measures a total of 45,496 ha of which barely 7,890 ha are covered with true forest (Bussmann 2002). The main reasons for forest destruction in the area are fires caused by honey-hunters and pastoralists, who burn the old grass at the start of the wet season. Others are overgrazing in the forest, and serving the firewood needs of a fast-growing population. Bytebier & Bussmann (2000) provide the first detailed vegetation description and checklist of the Mt. Nyiru flora, and Bussmann (2002) gives an overview on the forest vegetation of all of Kenya’s isolated smaller mountain ranges, and Bussmann (1994) as well as Bussmann & Beck (1995) provide an overview on the Mt. Kenya. The vegetation of Bale is covered by Friis (1986a, 1986b, 1986c), Friis (1992) and Bussmann (1997). The floristic diversity of all study areas is largely very similar, with the exception of the Sekenani-Maasai area, which includes only Savanna habitats.

THE LOCAL POPULATION

The Maasai

The Maasai are originally nomadic pastoralists. ‘Maasai’ indicates a speaker of the Maa language, which belongs to the Chari-Nile branch of the Nilo-Saharan language family. Maa speaking peoples migrated into their current territory around the 16th century (Ehret 1984). The Maasai are divided into eleven sections, each occupying specific areas. These sections show differences in dialect and ceremonial life (Ole Sankan 1995). At the end of the 19th century their original grazing territory encompassed almost 80% of Kenya and Northern Tanzania. In 1904/1911, the Il-Purko Maasai were moved south to the area around Narok (Ole Sankan 1995, Lamprey & Waller 1990) The Maasai in the Sekenani area belongs to this group. Now, many Maasai live a sedentary lifestyle. This change in settlement pattern has had a profound impact on the Maasai’s lifestyle and environment (Kiringe 2005, Lamprey & Reid 2004). Tourism has become a major economic force in Kenya in the last decades (Akama 1999).

The Maasai attribute most illnesses to the effect of pollutants that block or inhibit digestion. In most cases, the treatment of illness involves herbal purgatives to cleanse the patient. Early accounts of Maasai plant use date back to the beginning of the last century (Hollis 1905, Merker 1910). Studies on Maasai Ethnobotany of the Mara region have mainly focused on the forested areas of the Loita Hills (Kårehed & Odhult 1997, Maundu et al. 2001).

The Samburu

Like the Maasai, the Samburu are mostly nomadic pastoralists, inhabiting the plains and highlands of Northern Kenya. Like their cousins the Maasai, they speak a ‘Maa’ language. The Samburu occupy some of the northernmost parts of Kenya. This territory has always been – and still is, one of the remotest accessible areas of Kenya. Due to this remote location the Samburu, unlike the Maasai, received very little attention from the colonial administration. Independence changed this only marginally. For this reason the traditional way of nomadic life is still much more prevalent amongst the Samburu, who migrate from their lowland wet season grazing grounds up to the humid mountain areas in the dry season (Spencer 1965). Milk and blood from cows and soups derived from wild collected herbs are still the main pillars of Samburu diet. Especially children and women frequently eat berries and other wild fruits. Herbal knowledge is very widespread in the community, and many community members have an intricate knowledge of their environment. Studies on Samburu ethnobotany trace only back to the last two decades. Schultka & Hilger (1983) and Kokwaro & Herlocker (1982) provided some lists of Samburu plant use, while Heine et al. (1988) compiled the most detailed lists of the plant use of Samburu from various sources.

The Kikuyu

The Kikuyu are the largest single ethnic group in Kenya and account for 21% of the country’s population (Sindiga et al. 1995a, 1995b). In the recent past new interest in traditional herbal medicines has grown in this community. This may be attributed to high cost of modern drugs, inaccessibility of clinics and the fact that traditional medicine is regarded as effective and usually is the preferred mode of treatment for many illnesses especially in rural areas (Githae 1995). The study was conducted among smallholder farmers who play a major role in food production. Although the young people have absorbed large quantities of western culture, among the older people the remembrance of the past is alive. The values, attitudes and behaviours typical of the traditional life are in many cases still carefully and scrupulously followed (Bottignole 1984).

The Oromo

The Oromo are the main ethnic group in southern Ethiopia, including the Bale region, although members of many other peoples have settled in the area. Smaller populations are found in Somalia and northern Kenya. Barley and wheat cultivation provide most sustenance and income in Bale, with livestock keeping as additional activity. The Oromo language

belongs to the Cushitic language group like Maa. During the last decades, Bale has seen profound changes, from increased access and governmental health care entering during the communist era of the 1970s and 80s, to an increase in tourism in the 1990s and a large influx of Chinese development aid in the last few years. All of that is changing the local economy and customs profoundly.

MATERIALS AND METHODS

Plant collections

Fieldwork was carried out between 2001 and 2009 by Bussmann and collaborators amongst the Maasai (Sekenani), Kikuyu, Samburu and Oromo as follow up of an earlier vegetation ecological study covering this region. To record the identity of the plants used traditionally, interviews were conducted using semi-structured questionnaires, always using the same interview structure under the leadership of the present author. Random sampling technique was applied in distributing the questionnaires. Before carrying out the interviews, an oral prior informed consent was sought from every respondent. All communities involved showed the same acceptance of the researchers, and similar in-field times were involved in the study in order to avoid possible errors in data depth.

A total of 100 lay respondents (25 per tribal group) were interviewed. Access to female informants was only possible amongst the Kikuyu, while all other communities only allowed access to male informants. To allow comparability, only male informants are included in the present study. In order to get a more detailed inventory of plant use, ethnobotanical data were collected by interviews directly in the field during collection trips, and by discussing the freshly collected specimens with informants, after seeking oral consent from each respondent. This method was preferred over pure questionnaires to also get an indication for species that are not used by the community, and which are normally not mentioned during traditional interviews. All interviews were carried out in local language by native speakers, and then translated into English. Voucher specimens were collected and are preserved at the Jomo Kenyatta University herbarium, the East African

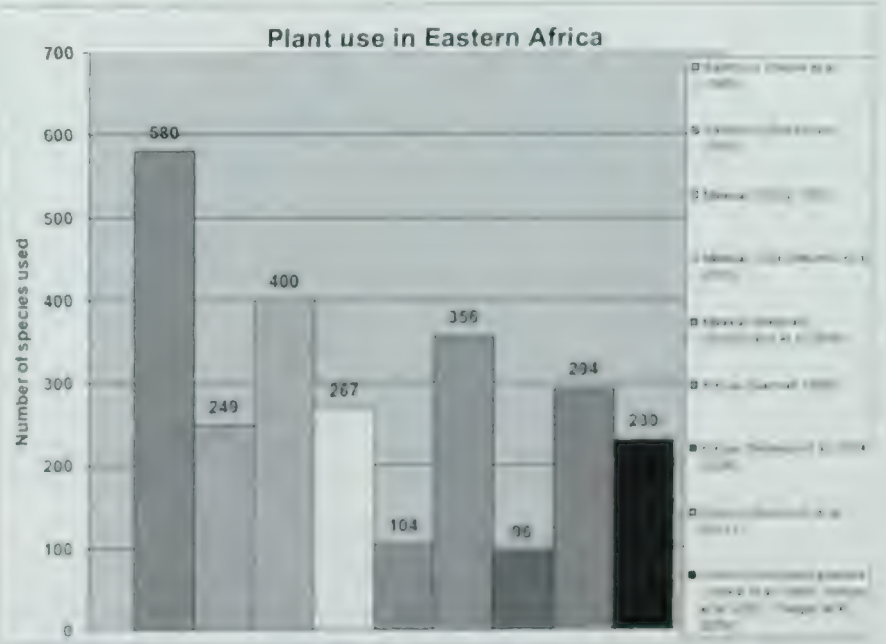


Figure 2 – Plant use in different ethnic groups

Herbarium (EA), University of Nairobi Herbarium, National Herbarium of Ethiopia (ADD), with duplicates at Missouri Botanical Garden (MO), Royal Botanic Gardens, Kew (K), University of Bayreuth (BT), the National Botanic Garden of Belgium, Meise (BR), and Stuttgart (STU). The identification of plant material followed the available parts of the Flora of Tropical East Africa (Polhill 1952–2010), the Flora of Ethiopia and Eritrea (Hedberg & Edwards 1989–2009) as well as. Agnew & Agnew (1994), Haines & Lye (1983), and Beentje (1994). Plant nomenclature followed TROPICOS (<http://www.tropicos.org>). Lists of all plants for all study areas have been published previously under open access (Bussmann 2006, Bussmann et al. 2006, Njoroge et al. 2004, Njoroge & Bussmann 2006a, 2006b, 2006c, 2007, 2009).

RESULTS AND DISCUSSION

The results obtained in our own studies (Bussmann 2006, Bussmann et al. 2006, Njoroge et al. 2004, Njoroge & Bussmann 2006a, 2006b, 2006c, 2007, 2009) are compared to each other as well as selected results of other colleagues (Maundu et al. 2001, Yineger et al. 2007, Lulekal et al. 2008, Yineger et al. 2008) from the same study regions. The latter three studies used expert-herbalists as informants, while all other studies focused on non-expert informants. This might account for some differences in the Oromo studies. Because detailed plant lists have already been published for all these studies, this material is not presented again in detail here.

Extent of plant usage

The Samburu of Mt. Nyiru attributed a use to 249 species (56%) of the local forest flora. This number is very close to the forest species reported in the compilation of Heine et al. (1988) who presented a list of 580 species of plants found in the Eastern part of the Samburu range, because the latter study included additional savanna areas, and thus a wider species portfolio. The number of plant species used (155) was significantly lower in the Sekenani Maasai area in the South of the country. A total of 155 plant species were collected in the Sekenani Valley (Bussmann et al. 2006). In comparison, 267 species were collected in the Loita Hills (Maundu et al. 2001). Both studies found a much lower plant number than researchers in the early 1900s (Hollis 1905). The Kikuyu inventory presented 96 species (Njoroge et al. 2004, Njoroge & Bussmann 2006a, 2006b, 2006c, 2007, 2009), which is much lower than the 356 species included in the Kikuyu plant use list compiled by Gachati (1989). The Oromo in Bale had names and to a large extent uses for 294 species (Bussmann et al. 2011), in comparison to a total of 230 species documented in the lower reaches of the Bale area (Lulekal et al. 2008), and 101 species in the highlands (Yineger et al. 2008) (fig. 2).

This clearly indicates that more traditional nomadic communities like the Samburu and Loita Maasai have retained higher plant knowledge than more westernized nomads like the Sekenani Maasai, and agricultural societies like the Kikuyu. The two Maasai groups make this transition clearly evident. When comparing different plant use categories, it becomes clear that in particular species originally used as medicines, food and to make tools, have drastically lost im-

portance in the more westernized Sekenani setting (fig. 3). In contrast, knowledge about fodder plants, ceremonially used species and construction material, to name a few examples, has been retained. The knowledge of the Oromo population in both the highlands of Bale and the lower areas south of the massif are similar.

Malaria

Malaria is very prevalent in many communities in Kenya, and the single most important condition treated with herbal remedies.

The Samburu used 28 species as treatment for malaria. Heine et al. (1988) found a very similar number of species used against malaria in their study area. This indicates that the treatment of this disease is still a high priority for the Samburu, and that plant use widely practiced in the different areas. The treatment normally involves the ingestion of a boiled extract of the remedy to induce strong vomiting and diarrhoea in order to purify the body. The Loita Maasai used fifteen species (Maundu et al. 2001), and the Sekenani Maasai use seven species (Bussmann et al. 2006). In comparison the Kikuyu used 58 species as anti-malarial herbal remedies, while the Oromo did not use a single species for this purpose. Although malaria occurs in the lowlands south of Bale, the Oromo population does not seem to treat malaria with plants there either (Lulekal et al. 2008) (fig. 4).

This result challenges our hypothesis that traditional societies retain more knowledge about medicinal species than more westernized societies. The differences between the Loita and Sekenani Maasai are expected, as is the fact that the Samburu still use mostly plants for malaria treatment. The surprising find is however that the most westernized agricultural group, living closest to big cities, has the largest portfolio of medicinal species against malaria. This suggests that transmission incidence in large populations is probably higher, and also suggests that western malaria medications are either too expensive, not safe to use on long term, or simply ineffective due to resistance. Thus, it is evident that societies

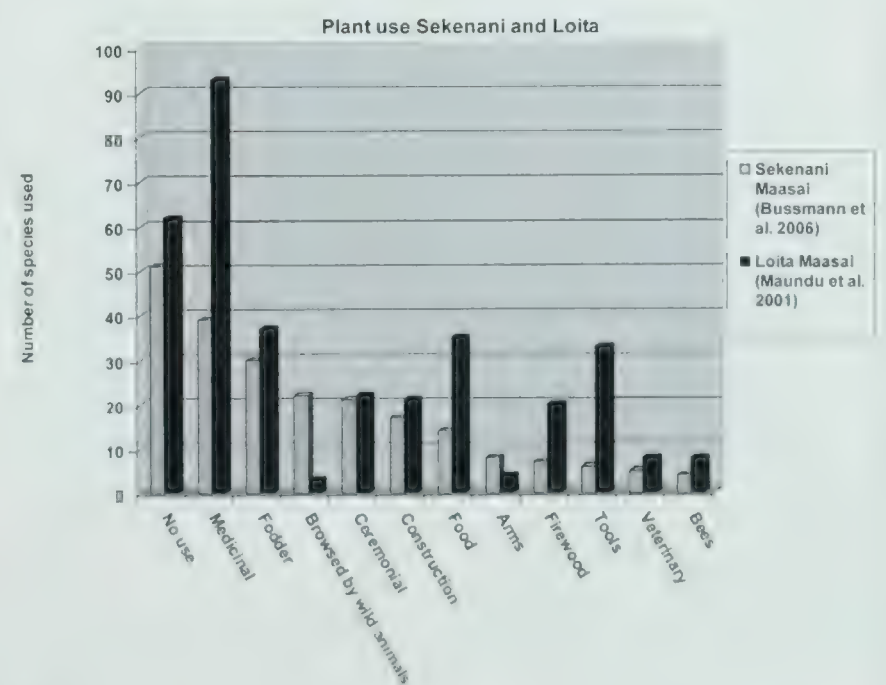


Figure 3 Comparison of traditional and westernized Maasai groups.

that have clearly lost a large part of their plant knowledge do tend to retain traditional knowledge if it serves a clear purpose.

Veterinary use

Astonishingly, hardly any veterinary use of plants was encountered amongst the Samburu and Maasai. Only five of the useful plant species were used as medicine for treatment of livestock diseases in Sekenani and amongst the Samburu, and eight in Loita. In contrast, eighteen species were used as veterinary medicine by the Oromo in this study, and forty plant species were regarded as useful in traditionally managing various diseases of cattle amongst the Kikuyu in Central Kenya (fig. 4). The results in Ethiopia in particular were very surprising, because Yineger et al. (2007) reported 74 veterinary medicinal plant species from the region, which is still less accessible than the upper parts of Bale.

This goes completely in contrary to our hypothesis that nomadic livestock herders would have a higher traditional knowledge of veterinary herbs. One possible explanation for this is however the fact that in striking contrast to medicinal care for people, governmental veterinary services seems to be much more available even in remote areas, where larger concentrations of livestock, and thus a higher susceptibility for diseases and epidemics merit making more services available, compared to the agricultural Kikuyu areas who only keep a few cows in their backyards. In addition, the value attributed to livestock is traditionally so high that scarce resources were rather spent on caring for livestock, while traditional medicines were mostly used for human consumption. The Kikuyu, closest to large population centers, were for this reason clearly neglected when it came to (free) governmental veterinary services, and had to rely on plant preparations, because they simply had no other choice.

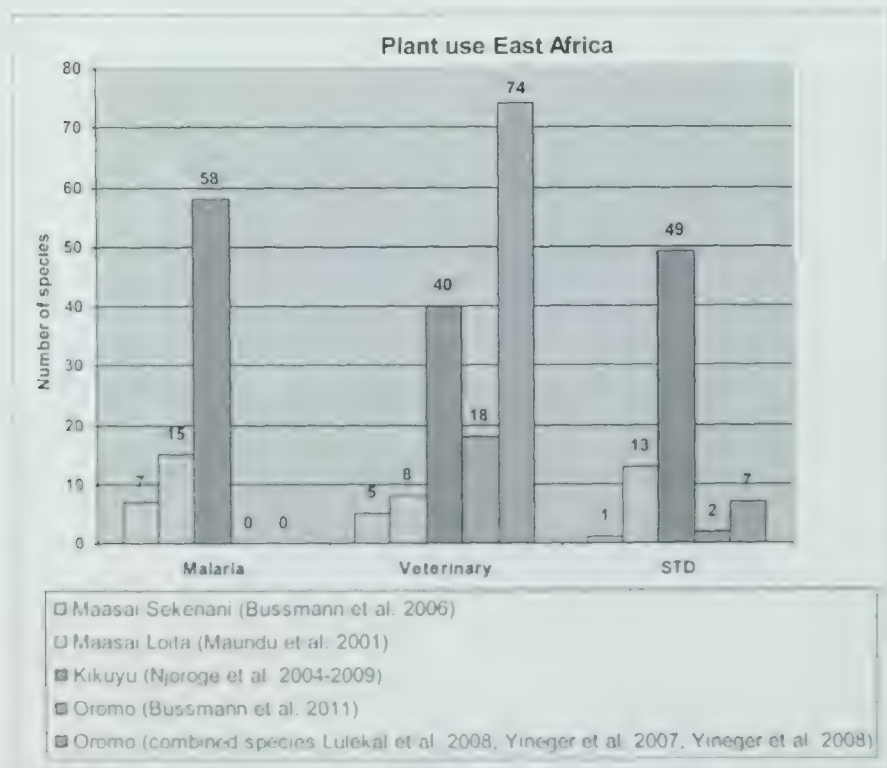


Figure 4 – Plant use in different ethnic groups – comparison of important diseases

Venereal disease

Plants for the cure of venereal diseases such as gonorrhea, syphilis and others, were almost not used by the Sekenani Maasai, amongst the Samburu, and amongst the present study in the Oromo area. Previous studies indicate that venereal diseases were amongst the most frequently treated with plants amongst the Oromo (Lulekal et al. 2008, Yineger et al. 2008). Plants used to treat STDs were also of significant importance in Loita, where thirteen species were used, and the Kikuyu again employed a vast number of species (49) for this purpose (fig. 4).

This again disproved our hypothesis that nomadic societies always have a higher knowledge of medicinal species. It appears that health care provided by NGOs and governmental health outposts has reduced traditional plant use for infectious diseases in remote areas. In addition, disease incidence is simply higher in densely populated areas with a large male migrant working population (Kikuyu). In addition, the stigma attached to STDs might prevent people from getting western medical care, or, in some cases, might simply have prevented the informants from sharing their knowledge. The reason for the profound difference in Oromo plant use lies probably in the fact that the comparative other studies used healers as informants, while the present study focused on laypeople.

CONCLUSIONS

Traditional plant knowledge has clearly declined over a large part of the research area. The most traditional groups still retain the greatest knowledge of plant use for human purposes, although societies in close contact to western culture are shown to retain a high plant usage in order to treat common ‘modern’ diseases as well as veterinary problems that are stigmatized, for which western medicinal treatment does not prove effective, or for which cheap treatment cannot be found. Western health care services as provided by governments and NGOs, in particular in rural areas, seem to have contributed to a decline in traditional knowledge, in part because the local population simply regards western medicine as more effective and safer, or as one of our Oromo informants put it “Sick people go to the clinic or cultural practitioner who prepares medicine from plants. Nowadays people mostly go to the clinic. Traditional herbalists are already very old. The tradition is normally passed from the father to the son. Formerly people came from far like from Addis, and there is still a woman healer who is famous for treatments for example for parasites. Western medicine is more scientific and thus more reliable. Traditional medicine is often very painful, and can cause harm. Sometimes people die of traditional medicine. For their animals people prefer to go to the animal hospital. Traditional remedies are only used for rabies.”

The comparative study indicated also a clear difference in plant knowledge between traditional healers and laypeople. This was most prevalent in Ethiopia, where the experts clearly had a much more profound knowledge than the non-experts interviewed.

ACKNOWLEDGEMENTS

The author would like to thank all their colleagues in Kenya and Ethiopia for their tireless support. The financial support for this work by the Murulle Foundation, The William L. Brown Center at Missouri Botanical Garden and the Deutsche Forschungsgemeinschaft (DFG) is acknowledged. The initial expedition to Mount Nyiru was funded by the Foundation for the Furtherance of Scientific Research in Africa (Belgium). Most of all, thanks to the population of Sekenani, Loita, central Kenya, Nyiro and Bale for sharing their tremendous ethnobotanical knowledge.

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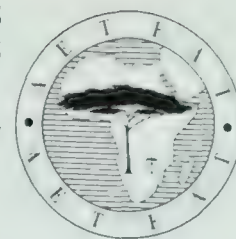
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Manuscript received 31 Aug. 2010; accepted in revised version 6 Jan. 2011.

Communicating Editor: Elmar Robbrecht.



Gloriosa superba (Colchicaceae): ethnobotany and economic importance

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Background and aims – *Gloriosa superba* L. (Colchicaceae) is a well known non-wood forest product and important medicinal plant widely used in several indigenous systems of medicine. Different pharmacological studies in a number of experiments have convincingly demonstrated the ability of *G. superba* to exhibit anti-inflammatory and antimicrobial activities lending support to the rationale behind several of its traditional ethnomedicinal uses. The present review is an up-to-date and comprehensive analysis of the traditional and folkloric uses of *G. superba* over its distributional range.

Methods – Herbarium, field and ethnobotanical studies were supplemented by a detailed literature review. Data on medicinal, poisonous and ornamental properties of *G. superba* were assembled together with linguistic aspects.

Key results – The pharmacological studies conducted so far on *G. superba* indicate the immense potential of this plant in the treatment of a wide range of ailments. Although the relative importance of *G. superba* varies by location, it is one of the most widely used plant species in the tropics, and is used in strikingly similar ways throughout its geographical range. The plant has escaped in several localities becoming naturalized, even a weed in some places; but it continues to be sold as an ornamental plant even in those areas where it is naturalized. In some parts of India, it is considered threatened due to over-harvesting by the pharmaceutical trade.

Conclusions – While there are gaps in the studies conducted so far, which need to be bridged in order to exploit the full medicinal potential of *G. superba*; it is still very clear that this widespread plant has tremendous potential for the future. On the basis of current information and evidence, *G. superba* extracts are characterized by instances of toxicity and with such potentially dangerous substances care in its use as medicine is essential to avoid complications of overdose.

Key words – Colchicine, ethnobotany, *Gloriosa superba*, horticulture, toxicity, weed.

INTRODUCTION

Gloriosa L. belongs to the family Colchicaceae, a horticulturally well known family of common garden ornamental herbs such as Bellworts (*Uvularia* spp.) and Naked Ladies (*Colchicum* spp.). The phylogeny and classification of the family Colchicaceae was recently investigated using cpDNA sequence data (Vinnersten & Manning 2007, Vinnersten & Reeves 2003). This study established the monophyly of the family as defined by Nordenstam (1998), composed of species with rhizomes, non-sheathing leaves, reticulate venation and berries. Members of Colchicaceae are known to contain the alkaloid colchicine, regarded as the biological hallmark of the family (Hegnauer 1963, Raffauf 1970, Vinnersten &

Larsson 2010, Wildman & Pursey 1968). Colchicine is today commercially extracted from *Gloriosa* and *Colchicum*.

More than forty species names of *Gloriosa* have been listed (IPNI 2011), although other authors (e.g. Dyer et al. 1962, Field 1971, 1972, Geerinck 2010, Hoenselaar 2005, Maroyi 2002, Thulin 1995, Wild 1965) regard *Gloriosa* as a monotypic genus, consisting of a single highly variable species, *G. superba*. The major variations in genus *Gloriosa* mainly involve plant height, flower shape, size and colour. Plant height varies from short and erect to long, slender, climbing on the surrounding vegetation to which it clings for support. The leaf tips are elongated into curling, twisting tendrils which twine around other vegetation and there are also plants without leaf tendrils, others with short or inconspicuous leaf

tendrils. Leaves in *Gloriosa* may be uniformly linear-lanceolate, lanceolate or broadly ovate. The short form normally has a single flower at the apex, while taller forms can carry many flowers, one in each of the upper leaf axils. Leaf arrangement is normally alternate, opposite, whorled or irregular or different combinations of phyllotaxis may exist on one plant. *Gloriosa* shows considerable amount of variation in its appearance, the perianth segments attain a full colour of either pure yellow or bi-coloured: red and yellow or purple and yellow. Plants with bi-coloured perianth segments tend to lose the yellow colour and turn either red or purple but the yellow tinge does not completely fade especially from the adaxial side. The perianth segments are variable in shape and size. There are two extreme forms of perianth segments: one which is heavily crisped and narrowly uniform throughout its entire length and broader, plane-margined perianth segments. With a large number of forms available for examination in one place, the differences are sometimes startling (Wild 1965). Variation is endless and one gets the impression that more than one species is involved (Wild 1965). The present authors are currently employing field investigations, biogeographical, morphological and molecular studies aimed at resolving the taxonomy of genus *Gloriosa*. It is clear that the genus needs taxonomical revision, given its traditional, present day and potential domestic and industrial uses. As the pharmaceutical industry research progresses, wide use of unpublished and doubtful names is creating problems and considerable taxonomic confusion. Therefore, this investigation is aimed at documenting traditional, folkloric and economic uses of *G. superba* over its distributional range.

MATERIALS AND METHODS

Literature review on traditional, folkloric and economic uses of *G. superba*

The study was conducted from 2007 to 2011. We began the present study by a literature review, in order to document traditional, folkloric and economic uses of *G. superba*. Records of uses of *G. superba* over its distributional range were identified during a review of over 200 multidisciplinary, mostly English language publications. Sources of information included: Bunyaphrathasara & van Valkenburg (1999), Burkill (1995), Dalziel (1955), Dounias (2006), Ganesan et al. (2007), Geetha et al. (2007), Gelfand et al. (1985), Ghani (1998), Haerdi (1964), Jagtap et al. (2006), Jain et al. (2004), Katewa et al. (2004), Neuwinger (1996), Prayoonrat (2005), Sandhya et al. (2006), Saralamp et al. (1996), Satri (1956), Sivakumar & Krishnamurthy (2002), Tiwari & Yadav (2003), Van Duong (1993), Van Steenis-Kruseman (1953), Watt & Breyer-Brandwijk (1962), Williams (1949), Yamanda (1999), Yineger & Yewhalaw (2007) and various Floras. An online literature search was also conducted using BioMed Central (www.biomedcentral.com), Blackwell Synergy (www.blackwell-synergy.com), CAB Abstracts (www.cabi.org), Elsevier Science Direct (www.sciencedirect.com), Ingenta Connect (www.ingentaconnect.com), ISI Web of knowledge (www.isiknowledge.com), intute (www.intute.ac.uk) and JSTOR (www.jstor.org) for scientific articles published before June 2011. References were also identified by searching the extensive library collections of the National Herbarium and

Botanic Gardens, Harare, Zimbabwe; Rhodes University, South Africa and Wageningen University, the Netherlands. Data collected from the literature included: use(s), mode of preparation, administration, and cultural uses of the species, if mentioned. Suitable books or potential literature sources were identified in online databases of the particular libraries by searching for the terms botanical medicine, cultural uses, economic uses, ethno botany, ethno medicine, folk medicine, folkloric uses, horticultural uses, indigenous medicine, traditional medicine of *Gloriosa superba*.

Herbarium and field studies

Over 1 200 herbarium specimens of *Gloriosa* on loan to the National Herbarium of the Netherlands, Wageningen branch (WAG) from the following herbaria: B, BM, BR, C, COI, F, K, L, P, S, U, UPS and collections kept in the following herbaria: SRGH and WAG (abbreviations follow Holmgren et al. 1990) were examined. Field studies were conducted in Zimbabwe between November 2007 and January 2011. Specific localities visited were determined from labels on herbarium specimens at the National Herbarium and Botanic Garden (SRGH) in Harare. These herbarium specimens were studied prior to field studies and during the course of the field work to obtain information on geographical distribution of *Gloriosa*, habitat, ecology, growth habit and determining its range of variation. As deduced from information given on herbarium labels and literature, *Gloriosa* in Zimbabwe tends to flower and/or fruit between November and May. Thus, fieldwork was conducted during this period.

Documentation of *G. superba* uses by both the rural and urban communities in Zimbabwe was also undertaken during field studies. This study utilised Participatory Rural Appraisal (PRA) (Chambers 1992, FAO 1989). This participatory approach provides a valuable insight into the multiple meanings, dimensions and experiences of local people with plant resources. It captures information that standard plant use methods are likely to miss. Use of open-ended methods, such as unstructured interviews and discussion groups allowed the emergence of issues and dimensions that are important to the community but not necessarily known to the researcher, thus allowing unanticipated themes to be explored by the interviewer (Miles & Huberman 1994). Prior informed consent was obtained orally before the start of each interview. All interviews were conducted in Shona, since the first author is a native speaker of the language. The process involved close consultation with the community in information sharing, data gathering and compilation. It involved visiting several villages, communities and discussing with many individuals the uses and cultural importance of *G. superba*. Purposive sampling was used in the selection of participants in order to allow us to have an in-depth focus on the issues important to the study (Cohen & Manion 1989).

RESULTS AND DISCUSSION

Geographical distribution

G. superba occurs naturally in subtropical, tropical Africa and Asia, and it is now naturalized in Fiji (Wright et al. 2005), the Réunion-Mascarene Archipelago (Tassin et al.

2007) and along parts of the Australian coast from north of Sydney to south-east Queensland (Groves et al. 2005). It is now invasive on Moreton Island and along the north coast of New South Wales (Groves et al. 2005, Le Cussan 2006), Lord Howe Island (Orchard 1994), French Polynesia Society Islands (Welsh 1998), Karibati Line Islands (Wester 1985), and Solomon Islands (Hancock & Henderson 1988). *G. superba* is cultivated throughout the world in many botanical and private gardens as an ornamental plant.

G. superba is important to people over the globe since 1600s or earlier, since it was included in some early floristic accounts (e.g. Adanson 1763, Crantz 1766, Herman 1687, Lamarck 1796). Miller (1768), in his Gardeners Dictionary, gave a hint on the deadly nature of *G. superba*, noting that “the root and every part of this plant is very poisonous, so should not be put in the way of the children”. By Miller’s time, *G. superba* was probably already a popular garden plant. The fact that both generic and specific names (i.e. *Gloriosa superba*) assigned by Linnaeus, describe the superb nature of the plant species means that we are dealing here with a beautiful ornamental plant of considerable antiquity. Explorers from Europe and Great Britain displayed some morphological forms of *G. superba* in the famous gardens at Kew, Chelsea Physic Garden in London and Amsterdam Botanic Gardens (Hoog 1950, O’Brien 1903, 1904). British, continental European and American nurserymen popularized and commercialized many colourful forms in the 18th and 19th centuries. Hundreds of cultivars (e.g. *Boom* 25374*, *Bracelin* 1490*, *Brumbach* 7401*, Hoog 1950, O’Brien 1903, 1904) have been developed as ornamentals for temperate climates. They are widely cultivated in America, Europe and Australia as garden flowers. It was introduced in Hawaiian Islands in the 19th century (Hillebrand 1888) and several forms from Central African countries and Equatorial Guinea

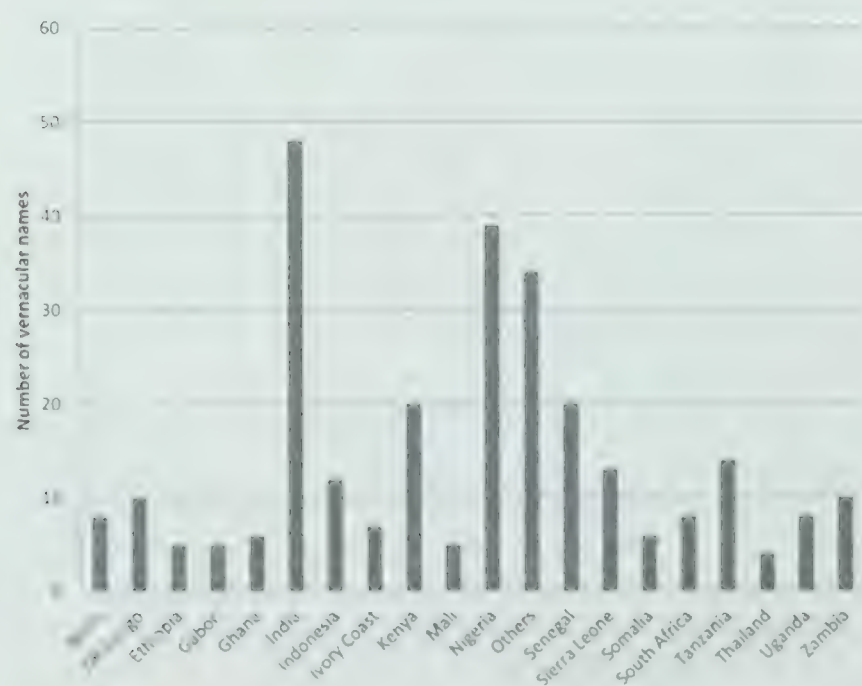


Figure 1 – Vernacular names of *G. superba*. Other countries with less than 4 vernacular names include: Bangladesh (1); Burkina Faso (2); Burundi (2), Cambodia (1); Cameroon (2); Central African Republic (3); Equatorial Guinea (1); Gambia (2); Guinea (1); Guinea-Bissau (2); Laos (1); Maldives (1); Mozambique (2); Namibia (2); Nepal (2); Rwanda (3); Sudan (1); Vietnam (2); Zanzibar (2) and Zimbabwe (2).

(Fernando Póo, now Bioko) were also introduced at Kew (O’Brien 1903, 1904). Quisumbing (1978) recorded *G. superba* as a recent introduction in the Philippines, where it is cultivated as an ornamental garden plant. The abundance of *G. superba* is recorded on herbarium labels as ranging from rare, occasional, and common to abundant. Where we have seen the plants in the field, for example in Malawi, South Africa, Zambia and Zimbabwe, they are in small patches, counting one to several individuals. *G. superba* is found from sea level to 2400 m altitude, growing in natural forests, thickets, savanna, and secondary or disturbed vegetation, hedgerows in which the lower part of the plant is shaded and the upper flower-bearing stems reach out for the sun.

Folkloric uses of *G. superba*

G. superba is known by a multiple of vernacular names (electronic appendix 1), which are not specific to any particular morphological type, form or any of the previously described species, but rather refer to *G. superba* sensu lato. Vernacular or common names of plants in some cases may indicate morphological features or may point to certain resemblances to other plants or to the agent of introduction or some cultural aspect. The introduction of *G. superba* to new localities, e.g. Australia resulted also in passing on of common names particularly English common names. These names may also aid in identifying the geographical origin of the species and the pathways of diffusion. Such informative names include Rhodesian Flame Lily, an English name widely used in Australia. This common name is describing the plant and at the same time the native country of the species (Rhodesia, now Zimbabwe), where it is the country’s national flower. *G. superba* was selected as the national flower of Southern Rhodesia (now Zimbabwe) in 1953, during the federation of Northern Rhodesia (now Zambia), Southern Rhodesia and Nyasaland (now Malawi). The design was chosen by Lord Llewellyn, the first Governor General of the Federation of Southern Rhodesia, Northern Rhodesia and Nyasaland “I have decided to use an African Flame Lily (*G. superba*) as the emblem, a flower of great beauty which grows naturally in each of the three territories”¹ (i.e. present-day Malawi, Zambia and Zimbabwe), which comprised the Federal area, i.e. the Federation of Rhodesia and Nyasaland.

Insight into the societal value of *G. superba* may be gained by examining the vernacular names of the species. People rarely name plant species that they do not use. A survey of herbarium specimens and the literature shows no fewer than 279 vernacular names for *G. superba* (electronic appendix 1, fig. 1). India, Nigeria, Kenya and Senegal appear to have the highest number of vernacular names (fig. 1). This long list of names indicates that local people in these countries have an active interest in *G. superba*. The plant is a well-known non-timber forest product that has long been in regular demand amongst local communities and practitioners of traditional medicines in different countries. In India, it is a much used plant in Ayurvedic and Unani systems of medicines (Chopra et al. 1956, Watt 1972), it is used either as

¹ National Archives of Zimbabwe (Reference F201/GG24)

* Collector of herbarium voucher, additional details in electronic appendix 2.

a single drug or in combination with other drugs. Although there are comments to the contrary, for example, reports from Vietnam indicating no known uses for the species (Van Duong 1993). This lack of ethnobotanical information from Vietnam may reflect no usage or that no one has studied or reported the usage of *G. superba* in that country.

Several of the plant's common names refer to the structure of the flowers, stems and tubers (electronic appendix 1). The indigenous people in Indonesia were inventive and imaginative; they recognised the reflexed nature of the flowers of *G. superba*, an invaluable diagnostic feature of the species. They described the flower shape and arrangement as unusual, hence the vernacular name *kembang sungsang*, which translates into "an upside down flower" (Maradjo 1977). The structure of the flower and flower colouration of red or purple and yellow resulted in *G. superba* being compared to a cow's tongue, rainbow, a crow's foot and a cock by local people in a couple of African countries. The Manding-Bambara people of Senegal call the species *donon tulu*, the Ndebele people of South Africa call it *amagugulume*, and the Ndebele and Shona people of Zimbabwe call it *amakukhulume* and *kajongwe* respectively. The common feature uniting all these vernacular names is their description of the colourful nature of *G. superba* resembling a cock's head. Other examples of vernacular names alluding to the plant's structure are those of the Somalis, the Basari of Guinea, the Fulani and Hausa of Nigeria. The Hausa people of northern Nigeria call *G. superba* *gatarin kurege* which translates into "ground squirrel's hatchet". *Adin tuki* is the name of the species in Northern Somalia, Warrangeleh, which appears to simply mean a "crow's leg" (Collenette 156*). In Guinea, the local name is *a-tiándiwú* which translates to "the rainbow in the sky" (Burkill 1995). The Fulani of Nigeria call the species *demnal nagge*, which translates into "cow's tongue". The last two names appear to be focusing more on flower colour than other characteristics of the inflorescence.

The flowers of *G. superba* have a long history of involvement with humans, throughout the distributional range of the species. Postage stamps bearing *G. superba* have been issued by the national governments of Democratic Republic of Congo, Gambia, India, Indonesia, Namibia, Uganda, Vietnam and Zimbabwe. Although the use of postage stamps is slowly fading away, it leaves an important historical cultural account of *G. superba* in both tropical Africa and Asia. The remarkable shape of the flowers evokes use as personal adornment; widely used in Kenya and Nigeria by placing over the ears (Burkill 1995). The flowers are also used by the Hindus in the worship of Siva and Lingam, whilst roots and tubers are reputed to possess medicinal properties and were included by the Sanskrit writers in the seven minor poisons of India; see the Pharmacographia Indica (Clewer et al. 1915). Lowrie (1903) wrote the following account on the attitude of Indians towards the plant "In hoeing the coffee, no Hindoo would root up or otherwise destroy this, to them, its a favourite plant and they (men and women) being passionately fond of flowers, might be seen working with their heads adorned with the beautiful bloom". *G. superba* is used in a similar way in Ghana, where two vernacular names, *patekodzo* and *samankantan*, allude to the use of the species as an adornment or bunting. Several vernacular names for *G. su-*

perba in African and Asian countries indicate a long history of human use in these regions. These names include those recorded by Farquhar (Farquhar 197*) in Nigeria and Tessmann (Tessmann 526*) in Equatorial Guinea.

Traditional uses of *G. superba*

G. superba is used for various ethnobotanical applications in many parts of the subtropics and tropics (table 1). Many similarities can be recognised when the uses of *G. superba* are considered in totality over its distributional range (table 1). This may be ascribed to shared cultural heritage on *G. superba* through exchange of its ethnobotanical information. The relations of people to their indigenous plants and that of other regions near or further away aids in measuring their cultural status and their contacts with each other (Gilmore 1932). By carrying out such studies we gain knowledge of the pattern of their life customs and habits of life; and we also obtain suggestions for additional uses of plants besides those now employed by the local people. For example, in the past people may have depended on *G. superba* for a couple of medicinal uses, before better remedies from other plant products became readily available on the market. The development of the human race has meant that some of the uses of *G. superba* are no longer appreciated and such knowledge is in danger of being lost. So when such information is recorded, it does not mean that it is current practice, but reminds people of the potential of the species in their daily lives. The purposes for which people grow, nurture and move *G. superba* are varied; with even some reports of the tubers being eaten in Maldives (Munch-Petersen 80*, Schmelzer 84*). Tubers are said to be eaten when fried with sugar added to them (Schmelzer 84*).

G. superba as a commercial source of colchicine

Clewer et al. (1915) isolated a mixture of alkaloids consisting mainly of colchicine from dried tubers of *G. superba*. Colchicine yield from *Colchicum* and *Gloriosa* has been compared (Bunyaphatsara & van Valkenburg 1999, Jha et al. 2005). On dry mass basis, *Colchicum* yielded 0.62% colchicine and 0.39% colchicoside, while *Gloriosa* yielded 0.9% and 0.82% respectively (Jha et al. 2005). The seeds are valued as a commercial source of colchicine. The tubers also contain colchicine, but the content in seeds is reported to be up to ten times higher, hence the importance attached to good seed set when the plant is grown for colchicine production (Bunyaphatsara & van Valkenburg 1999). A report from Rwanda claims that the highest colchicine content is present in the young leaves (Neuwinger 1996). The seeds of *G. superba* are highly priced in the world market as they are the main sources of colchicine (Sivakumar & Krishnamurthy 2002).

G. superba as a weed

G. superba has been recorded as a farmland weed in West Africa (Burkill 1995) and also as an agricultural weed in Thailand (Prayoonrat 2005). It was identified as naturalized at Caloundra in south-east Queensland in 1950 and in New South Wales in 1972 (Groves et al. 2005). Other publications

Table 1 – Traditional uses of *Gloriosa superba*.

Country	Part used and recipe	References
Bangladesh	Tuber paste applied externally for parasitic skin diseases. Also used as an abortifacient, remedy for fever and asthma.	Ghani 1998, Sayeed Hassan & Roy 2005, Siddique et al. 2004
Burkina Faso	Leaves administered in enema as a decongestant.	Dounias 2006
Burma (Myanmar)	Tuber used as a murder poison and to commit suicide.	Bunyaphrathatsara & van Valkenburg 1999, Dalziel 1955, Neuwinger 1996
Burundi	Leaf decoction prescribed for hydrocele (dropsy of the scrotum), while the leaf pulp serves against rheumatism and mental patients are given a leaf decoction in a drink.	Dounias 2006
Cambodia	Used as a poison.	Bunyaphrathatsara & van Valkenburg 1999
Cameroon	The unripe fruit in butter used in north Cameroon to kill head lice.	Neuwinger 1996
Congo (Brazzaville)	Soup of leaves with a kid's heart is administered for female sterility or for delayed child-birth, and crushed leaves applied to the chest for asthma together with charred roots taken internally.	Burkill 1995, Dounias 2006
DR Congo (Kinshasa)	Rasped and washed tuber used externally to treat venereal diseases and stomach ache. <i>G. superba</i> cause losses among grazing animals every year in the Shaba province between dry and rainy seasons (October to December). Local people discouraged to eat buds of the species since it is poisonous.	Dounias 2006, Neuwinger 1996, Yamanda 1999
Ethiopia	Dried powdered root administered with tea or coffee as remedy for tumour.	Yineger & Yewhalaw 2007
Gabon	<i>G. superba</i> generally regarded as poisonous. Fang hunters are reported to eat the leaves chopped up with seeds of a small pumpkin and meat of a pig as an exercise in magic to bring luck in hunting warthog. Tuber macerate used to kill head lice.	Burkill 1995, Neuwinger 1996
Ghana	<i>G. superba</i> regarded as a danger to grazing stock and the Gbe-Vhe name is <i>haduihaku</i> : if a pig eats it, he will die. Grazers in Kordofan are reported to pull up the plant and burn the tubers to keep down the plant population. Juice of crushed leaves is used to kill head-lice.	Burkill 1995, Dalziel 1955
Guinea	<i>G. superba</i> regarded as poisonous but people make poultices of them to relieve neuralgias; and juice of crushed leaves is used to kill head-lice.	Dalziel 1955, Neuwinger 1996
Guyana	Leaf extract used against head lice.	Maradjo 1977
India	Tuber paste used as an abortifacient and as an ecboic in labour. Paste of dried tuber applied on wounds. Tuber generally regarded as a purgative, an anthelmintic and used to cure leprosy. Root found useful against colics, chronic ulcers and haemorrhoids and the white starchy powder obtained after repeated grinding and washing given for gonorrhoea. Commonly put on windows to keep snakes away. Macerated root used in lotion form to kill skin-parasites and head lice. Tuber paste applied externally to cure tumours and the root crushed and applied on Mayang cattle to treat prolapse. Tubers used as a murder poison, regarded as dangerous to grazing stock and used to poison cattle.	Dalziel 1955, Geetha et al. 2007, Jagtap et al. 2006, Jain et al. 2004, Katewa et al. 2004, Neuwinger 1996, Sandhya et al. 2006, Satri 1956, Tiwari & Yadav 2003
Indonesia	Often planted as an ornamental or hedge. Also used against head lice.	Maradjo 1977
Iran	Used for impotence and nocturnal seminal emission.	Burkill 1995
Ivory Coast	Tuber used against female sterility and as an aphrodisiac. Leaf decoction used as a liniment to ease coughs and general pain. Leaf juice inserted into the nose as a remedy for fainting fits. Pulped leaves administered as enema for pelvic decongestant. Believed to have magical properties as it is credited with the ability to cause poisoning at a distance.	Burkill 1995, Neuwinger 1996
Kenya	The Marakwet people take tuber decoction against abdominal disorders and to induce abortion. Root boiled and taken as medicinal tea against stomachache. Macerated tuber also taken against smallpox, leprosy, eczema, itch and ringworm. Powdered tuber used as a suicidal agent and to commit homicide. Tuber used for impotence and as an abortifacient. Cattle bitten by snake made to inhale the vapour of stewed roots.	Dounias 2006, Neuwinger 1996
Maldives	Washed root is eaten, fried with sugar.	Munch-Petersen 80*, Schmelzer 84*

Table 1 (continued) – Traditional uses of *Gloriosa superba*.

Country	Part used and recipe	References
Mozambique	Tubers regarded as poisonous. Roots boiled and given to nursing babies when they have stomach pains.	<i>Faulkner</i> 361*, Watt & Breyer-Brandwijk 1962
Nepal	Tuber is tonic, antiperiodic, laxative, purgative and stomachic. Tuber juice given for hysteria and abdominal disorders. Root considered abortifacient. Leaf juice and tubers used to treat skin diseases and bowel complaints.	Manandhar 2002
Nigeria	Tuber added to arrow poison, used as suicidal agent and to commit homicide. Yoruba name, ewé-ajé, means “leaf of the sorcerer”, and used to prevent one from being poisoned. The Igbo in southeast Nigeria drink tuber extract against anthritis. The pulped root is used in topical application for arthritic conditions, sprains and dislocations. The root is used as an antidotal to snake-bite.	Burkill 1995, Dounias 2006, Neuwinger 1996,
Senegal	<i>G. superba</i> regarded as poisonous, leaf-sap used in arrow-poisons. But people make poultices of the leaves to relieve neuralgias and leaf juice used to kill head-lice.	Burkill 1995, Dalziel 1955
Sierra Leone	Leaf decoction applied as liniment to ease cough and general pain. Leaf juice instilled into the nose in case of fainting and also administered in enema as a decongestant.	Dounias 2006
Somalia	Used as remedy against snake bites.	Burkill 1995, Synnott JESS 449*, Thulin 1995
South Africa	Tubers regarded as poisonous, but used as a cure for impotence and barrenness. Also used as an antiparasitic and a remedy for ascites, skin eruptions, charm, lice killer; tick infections and screw-worm on cattle; and to determine the desired sex of a child.	McGaw & Eloff 2008, Roberts 1990, Watt & Breyer-Brandwijk 1962
Sri Lanka	Tuber paste used as an abortifacient, applied for skin disorders such as warts or blackheads, scorpion bites, sprains and dislocations. Tuber used as a murder poison.	Burkill 1995, Neuwinger 1996
Sudan	Tuber sap used as an ingredient of a drink that induces sleep.	Dounias 2006
Tanzania	Plant sap drunk as a remedy for malaria, impotence and abortifacient. The Ulanga people burn the herb and apply ash on wounds to promote healing. The Ulanga people also use tuber juice for ear drops to treat earache. Powdered tuber commonly used as a suicidal agent and to commit homicide. Roots put in water with leaves and taken orally as treatment for small pox and swelling of the joints. Sukuma people also remove <i>G. superba</i> plant appearing near to their houses as it is believed to attract lightning.	Burkill 1995, Dounias 2006, Haerdi 1964, Neuwinger 1996, Tanner 1364*
Thailand	Root is a popular medicine for cancer, analgesic and treatment of acute gout. But not recommended as herbal medicine due to low therapeutic dose which is close to toxic dose.	Saralamp et al. 1996
Uganda.	Banyankole girls apply root-pulp of <i>G. superba</i> to their breasts to make them larger. Rhizome preparation used to treat for impotence and as an abortifacient.	Haerdi 1964, Purseglove 435*
Vietnam	Not used medicinally in folk medicine, perhaps because of its high toxicity	Van Duong 1993
Zambia	Tuber is part of a preparation to cure impotence and used as an abortifacient. Powdered tuber is a criminal poison and suicide poison in south Zambia. <i>G. superba</i> is also used against gonorrhoea and snake bite.	Dounias 2006, Fowler 2007, Neuwinger 1996
Zanzibar	Stem cut and used in villages as a rough pen, hence a Swahili name for the plant <i>kalamu</i> : a pen or pencil	Williams 1949
Zimbabwe	Well-known poisonous plant. Used as a remedy for toothache by the Shona people. Tuber used as an aphrodisiac. Sold along major highways as a cut flower.	Gelfand et al. 1985, Mavi 1996

list it as an ornamental plant, garden escape, naturalized, weed or environmental weed in Australia (e.g. Conran 1987, Le Cussan 2006) and Fiji (Wright et al. 2005). Farmers in Kordofan, Sudan are reported to pull up the plant and burn the tubers to keep down the population (Burkill 1995). *G. superba* seems to be invasive in coastal areas of Australia. It reproduces vegetatively by persistent tubers which re-shoot even when the foliage has been removed. It forms dense infestations in coastal areas, excluding or displacing native plants. It has been declared a noxious weed in some parts of Australia, e.g. Lord Lowe Islands, where severe infestations

of 100 stems/m² have been recorded (www.northcoastweeds.org.au). Due to the invasive ability of *G. superba*, range management procedures have been initiated which now include the monitoring and control of the species. It is one of the most difficult coastal weeds to control. The most effective control in Australia has been achieved using foliar spray application with glyphosate and metsulfuron-methyl in late November or December (depending on the season) when the new annual stems first appear (www.northcoastweeds.org.au). A follow up application in February or March, has also proved effective. Home-owners in Australia are under pres-

sure from the local authorities to use all manual, mechanical and chemical means to eradicate it for the safety of children. Those with *G. superba* growing in their gardens are urged to dig up the tubers and destroy the plants.

Horticultural potential of *G. superba*

G. superba is an increasingly important species for its horticultural and floricultural uses. In recent years, a number of cultivars have been used as ornamentals in the USA and Europe (Bose et al. 2003). *G. superba* can be grown as a house or outdoor plant; but it is unlikely to flower outside in Europe. It dies down when the weather gets cold. *G. rothschildiana* is one of the prettiest cultivars of *G. superba*. This cultivar was named after Baron Z.W. Rothschild, an authority on birds, who bought the flower from Africa and entered it at an exhibition of the English Horticultural Society at the turn of the previous century (Bose et al. 2003). It was first cultivated in the United Kingdom in 1902 (O'Brien 1903), now mainly grown in Belgium (*Boom* 25374*), Denmark (*Botanical Garden of Copenhagen* 1967*), the Netherlands (*Boom* 25374*) and the United States of America (*Bracelin* 1490*, *Brumbach* 7401*, *Schallert* 23145*).

G. superba is characterised by poor seed germination, susceptibility towards many pests and excessive collection in habitats for both medicinal uses and pharmaceutical trade (Dounias 2006). Therefore, in order to provide enough plant material for commercial exploitation, cultivation of the species at a large scale is necessary. In horticultural practice, vegetative propagation of *G. superba* is commonly used but the growth is very slow (Krause 1986), multiplication rate is low as only two plants are produced per corm per year. It takes four or five vegetative cycles to complete a reproductive phase (Samarajeewa et al. 1993). The effect of different growth regulators on initiation and multiplication of *G. superba* shoots in tissue culture have been studied by many researchers (Finnie & Van Staden 1991, 1994, Sivakumar & Krishnamurthy 2002). The tissue culture production of resting organs such as tubers is very important as they adapt easily after they have been transplanted to soil (Kozak 2002). In-vitro tubers have several advantages, they are hardier, easier to handle, can be transported dry and there is no dormancy period (Jha et al. 2005), thereby making year-round cultivation possible.

Conservation status of *G. superba*

Due to its multiple uses, the demand for *G. superba* is constantly on the rise, particularly in India. India is a major exporter of raw medicinal and aromatic plants (MAPs) as well as processed plant-based drugs (Lambert et al. 1997). This boom in export trade, involving *G. superba* and other plant species is depleting these resources from the wild, bringing some to the edge of extinction. Current harvesting practices in Bangladesh (Ghani 1998, Siddique et al. 2004) and India (Jha et al. 2005, Raina & Gupta 1999) are unsustainable and have resulted in depletion of the plant resource base. Earlier, the medicinal properties of *G. superba* were thought to be present only in the tubers (Raina & Gupta 1999) and these were ruthlessly extracted. As a result of scarcity and increased demand for its crude and processed products, *G.*

superba has been placed on the negative list of exports by the Ministry of Commerce, Government of India (Raina & Gupta 1999).

Zimbabwe is the other country where *G. superba* is protected. It is the country's national flower and is protected under the Parks and Wildlife Act enacted in 1975, therefore, it cannot be collected from the wild without a permit from the Department of National Parks and Wildlife Management. This is a precautionary measure, as *G. superba* is not threatened, but plant collectors and flower vendors, poach *G. superba* flowers from national parks, private and state land. These intermediaries sell the flowers in the city streets and along major highways.

CONCLUSION

This study resulted in the collection and documentation of scattered information on traditional, folkloric and economic importance of *G. superba* over its distributional range. Useful information was generated as a result of linking modern ethnobotanical studies with traditional or historical ethnobotanical approaches. This species is not only used for cultural purposes and as herbal medicine but it is also a notorious human and livestock poison. Its tubers have been used for centuries for homicide, suicide and inducing abortion. There is no doubt, however, that *G. superba* can constitute an important source of active molecules useful as raw material for the pharmaceutical industry.

SUPPLEMENTARY DATA

Supplementary data are available in pdf at the Supplementary Data Site of publications from the National Botanic Garden of Belgium (<http://www.nbgpublisher.be> > SBB50 > folder 495) and consist of the following: (1) list of vernacular names of *Gloriosa superba* and (2) collectors and source of herbarium vouchers referred to in the text, in table 1 and in electronic appendix 1.

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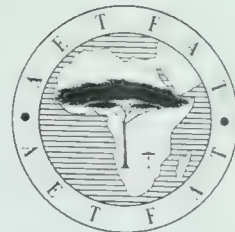
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Manuscript received 3 Aug. 2010; accepted in revised version 11 Oct. 2010.

Communicating Editor: Rainer Bussmann



Jean Léonard (1920–2013), cofondateur et cheville ouvrière de l'AETFAT

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Les trois fondateurs de l'AETFAT, à la VI^e réunion plénière de l'AETFAT à Uppsala en septembre 1966: de gauche à droite, Jean Léonard (1920–2013), Arthur Wallis Exell (1901–1993) et Milne Redhead (1906–1996).

En 1945, jeune botaniste diplômé de l'Université libre de Bruxelles, Jean Léonard signe son premier contrat à l'Institut national pour l'étude agronomique du Congo (INEAC). Il s'embarque alors pour le Congo belge où il est chargé de la préparation de la famille des Ranunculaceae pour la *Flore du Congo belge et du Ruanda-Urundi*. Très vite il perçoit l'intérêt de résoudre les problèmes systématiques et taxonomiques en concertation avec ses collègues travaillant sur la même famille dans des territoires voisins. Il contacte alors Arthur Wallis Exell (1901–1993), conservateur de l'herbier du British Museum, qui avait traité cette famille dans le *Conspectus Florae Angolensis*, et Milne Redhead (1906–1996), responsable de la section "Afrique tropicale" de l'herbier des jardins botaniques de Kew, qui l'avait étudiée pour le *Flora of Tropical East Africa*. De retour en Europe à l'issue de son premier terme de trois ans dans la colonie belge, il les rencontre à Londres en septembre 1950.

De cette rencontre est née l'idée de fédérer les botanistes confrontés à la prolifération des travaux consacrés à la flore de l'Afrique au sud du Sahara. C'est ainsi qu'en décembre 1950, sous l'impulsion de Jean Léonard, et de ses deux collègues britanniques, est née l'Association pour l'Étude taxonomique de la Flore d'Afrique Tropicale (AETFAT), forum destiné à promouvoir la coopération et la communication entre botanistes taxonomistes s'intéressant à la flore de l'Afrique tropicale.

En octobre 1951, est organisé, à l'Institut de botanique de l'Université libre de Bruxelles, le premier symposium de l'AETFAT qui rassemble une trentaine de participants sur les quelque 200 membres que compte déjà l'association fondée moins d'un an auparavant. Dès 1953, Jean Léonard entreprend de compiler le relevé des travaux de phanérogamie systématique et des taxons nouveaux concernant l'Afrique au sud du Sahara, relevé qu'il publie annuellement sous le titre *AETFAT Index*, jusqu'en 1976. Durant toutes ces années, toujours actif sur le terrain comme dans les herbiers du Jardin botanique national de Belgique, il participe très régulièrement aux réunions triennales de l'AETFAT et, en tant que secrétaire permanent, il assure le lien entre ses secrétaires généraux successifs jusqu'en 1988. Sa retraite, trois ans auparavant en 1985, n'avait pas mis fin à son activité de botaniste. loin de là : il a continué à travailler au Jardin botanique national de Belgique jusqu'en 2000, où Meise accueillit le 16^e congrès de l'AETFAT.

Par son engagement, sa rigueur scientifique et sa convivialité, Jean Léonard a posé les bases, il y a plus d'un demi-siècle, d'une association qui compte aujourd'hui quelque 1000 membres issus des pays du Nord et du Sud, et dont les congrès rassemblent plusieurs centaines de botanistes qui collaborent à l'étude et à la préservation de la biodiversité en Afrique.

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The editors kindly acknowledge the assistance of the following external reviewers
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*Les éditeurs remercient les relecteurs externes suivants
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For a number of years now, MOABI furnishes small grants to help young scientists. This is usually done by supplying a financial contribution to make a study visit, visit a congress, especially the AETFAT congress, or finish a paper. The fund is supported by individuals only and therefore the number of small grants has to be limited. The criteria for eligibility are posted on the website. During the AETFAT 2010 meeting a small number of young scientists could be supported again and attended the congress.

In addition, in 2010 the MOABI Foundation has decided to provide two specific awards, one for the best poster presentation and one for the best oral contribution, to young researchers visiting the AETFAT Congress. The Moabi Awards, consisting of a small amount in cash as well as a certificate, were awarded for the first time at the XIXth AETFAT Congress. After careful selection the evaluation team decided to award the following two prizes:

Best poster: Catherine Masao, University of Dar es Salaam, Genetic diversity, evolutionary history and conservation of giant lobelias in eastern Africa. "A sound piece of research, presented in a pleasant and clear way, dealing with a group of splendid plants, on a very nicely formatted poster".

Best presentation: Germinal Rouhan, MNHN, Paris, Systématique et évolution de la flore ptéridologique-malgache : l'exemple du genre *Elaphoglossum* (Dryopteridaceae). "Enthusiastically presented, high information content, implications for phylogeny, biogeography and taxonomy, in a splendidly illustrated and animated presentation."

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N. Beau, S. Dessein, E. Robbrecht (editors)

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Proceedings of the XIXth AETFAT Congress,
held at Antananarivo, Madagascar, 26–30 April 2010

Diversité des Plantes africaines
Systématique et Développement Durable
Actes du XIX^e Congrès AETFAT,
tenu à Antananarivo, Madagascar, 26–30 Avril 2010



This volume assembles fifty papers from the nineteenth Congress of the “Association pour l’Étude Taxonomique de la Flore d’Afrique Tropicale”. Most of the twelve symposia held during the Congress are represented by the themes in these Proceedings: Global change, Conservation, Ecology and vegetation, Systematics, Phytogeography, Floristics, Databases, Sustainable use, and Ethnobotany.

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ISBN 9789072619921

ISSN 0779-2387

D/2013/0325/003

